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CONTENTS

Volume 5 Number 1 March, 1966

Forelegs of Butterflies I. Introduction: Chemoreception Richard M. Fox	1
A New Species of <i>Epinotia</i> Hubner from British Columbia (Olethreutidae) T. N. Freeman	13
Studies in the Life Histories of North American Lepidoptera California <i>Annaphila</i> II. J. A. Comstock and C. Henne	15
New Skipper Records for Mexico H. A. Freeman	27
A Moth Sheet Noel McFarland	29
Cover Photo: <i>Daritis</i> ? <i>howardi</i> Hy. Edw. larvae Noel McFarland	36
Rediscovery of <i>Annaphila casta</i> Hy. Edw. in California (Noctuidae) John S. Buckett	37
Studies on the Nearctic <i>Euchloe</i> . Parts I, II Paul A. Opler	39
Butterfly Aggregations Walfried J. Reinthal	51

Volume 5 Number 2 June, 1966

Morphology of the Immature Stages of <i>Everes Comyntas</i> Godart Donald A. Lawrence and John C. Downey	61
A Little-Recognised Species of <i>Heliconius</i> Butterfly John R. G. Turner	97
Comparative Speciation In Two Butterfly Families, Pieridae and Nymphalidae Björn Petersen	113
The Butterfly Fauna of a Yellow Pine Forest Community Oakley Shields	127

Laboratory Techniques for Maintaining Cultures of the Monarch Butterfly	F. A. Urquhart and R. W. Stegner	129
Vital Staining of <i>Colias philodice</i> and <i>C. eurytheme</i>	John M. Kolyer	137
The North American Species of the Genus <i>Zeiraphera</i>	A. Mutuura and T. N. Freeman	153
Notes on <i>Eacles penelope</i> (Saturniidae)	Brian O. C. Gardiner	177
Remarks on The Genus <i>Zera</i> Evans in Mexico with a New Record	H. A. Freeman	181
Studies on the Nearctic <i>Euchloe</i>		
Part 3. Complete Synonymical Treatment		185
Part 4. Type Data and Type Locality Restrictions	Paul A. Opler	190

Volume 5 Number 4 December, 1966

A New Species of <i>Oncocnemis</i> from the Western United States (Noctuidae:Cucullinae)	John S. Buckett and William R. Bauer	197
Speciation in the <i>Agathymus</i> (Megathymidae)	H. A. Freeman	209
The Eggs and First Instar Larvae of Three California Moths	John Adams Comstock	215
An Additional Food Plant Record for <i>Papilio thoas</i> <i>autocles</i> R. & J.	John Adams Comstock	220
A New Species of <i>Polia</i> Ochseneheimer from California and Notes on <i>Polia discalis</i> (Grote) (Noctuidae:Hadeninae)	John S. Buckett and William R. Pauer	221
Know Your Author — Brian O. C. Gardiner		229
A Gynandromorph of <i>Lycaena gorgon</i>	Paul A. Opler	230
The Distribution and Bionomics of Arctic-Alpine <i>Lycaena</i> <i>phlaeas</i> Subspecies in North America	Oakley Shields and Johnson C. Montgomery	231
Three Western Species of <i>Polites</i>	E. J. Newcomer	243
Know Your Author — Bryant Mather		248
Overcoming Difficulties With The Pupae of <i>Euproserpinus</i> <i>phaeton mojave</i>	Noel McFarland	249
<i>Speyeria cybele</i> In Mississippi. Argynninae: (Argynnis)	Bryant Mather	253
<i>Euphyes dukesi</i> — Additional Record	Bryant Mather	254
The Little Known Moth <i>Euxoa sculptilis</i> (Harvey) in Arizona, with Descriptions, Illustrations, and Notes on <i>Euxoa violaris</i> (Grote and Robinson) (Noctuidae- Agrotiinae)	J. S. Buckett	255
Discovery of A Larval Hostplant for <i>Annaphila lithosina</i> With Notes on the Species (Noctuidae Amphipyrrinae)	John S. Buckett	262
Appendix to Distribution of <i>Lycaena phlaeas</i>	Oakley Shields and Johnson C. Montgomery	265
Correction to "A Little-recognized Species of <i>Heliconius</i> Butterfly"	John R. G. Turner	267

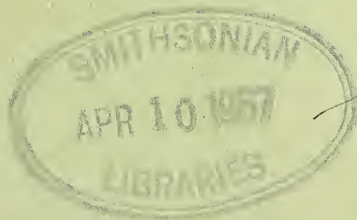
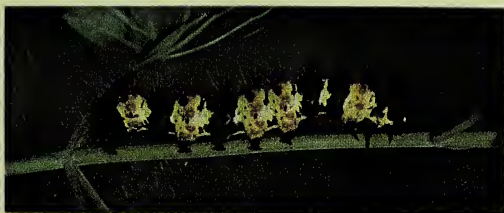
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THE PURPOSE OF THE JOURNAL is to combine in one source the work in this field for the aid of students of this group of insects in a way not at present available. THE JOURNAL will attempt to publish primarily only critical and complete papers of an analytical nature, though there will be a limited section devoted to shorter papers and notes. QUALITY WORK on any aspects of research on the Lepidoptera is invited. Analytical and well illustrated works are preferred, with a minimum of long description.

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FORELEGS OF BUTTERFLIES I.

INTRODUCTION: CHEMORECEPTION.

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THIS STUDY, planned as the first of a short series on butterfly forelegs, considers some general questions raised by peculiarities of these appendages, briefly reviews evidence for chemoreception by the legs of butterflies and presents a preliminary investigation of an additional chemoreceptive function. Subsequent studies will be concerned with morphologic homologies, taxonomic correlations and with function.

It is a pleasure to acknowledge the assistance of Albert Lloyd, John Bauer, Richard T. Satterwhite — who also prepared the drawings — and Jean Walker Fox, all of Carnegie Museum, in collecting live material for study, and of Clifford F. Thompson, graduate student at the University of Pittsburgh, in preparing serial sections for me. I am particularly grateful to Dr. Vincent G. Dethier for reading a preliminary version of this paper and for his very useful suggestions.

It is also a pleasure to acknowledge the support of my research by National Science Foundation through grants GB-510 and GB-2928.

SOME GENERAL CONSIDERATIONS

The degree of reduction in size of the prothoracic legs and differences in reduction between the sexes have traditionally been among the principal characters used to define the major butterfly taxa — the four superfamilies as presented by Fox *et al.* (1965), sometimes ranked as families: Hesperioidea, Papilionoidea, Nymphaloidea and Lycaenoidea. My reasons for using superfamilies have been discussed elsewhere (Fox *et al.*, 1965: 44-46).

The primitive condition probably was one in which all three pairs of legs were of about the same size and each leg had all five tarsal subsegments and a post-tarus bearing claws and certain median structures (see Fox and Fox, 1964: 71-72). Among butterflies, reduction of forelegs occurs in two different ways:

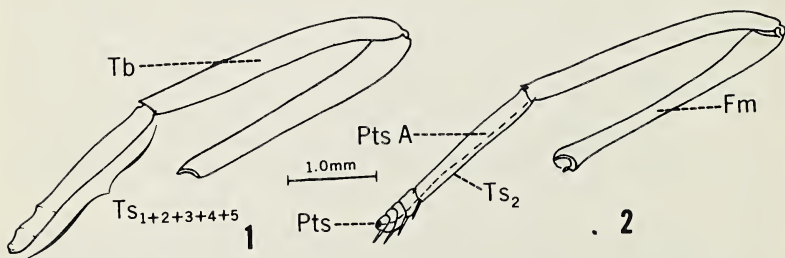
(1) miniaturization without loss of any part, and (2) miniaturization along with reduction through fusion in the apparent number of tarsal subsegments, plus the real or apparent loss of the post-tarsus and, in a few extreme cases, reduction in proportionate size of the tibia.

Reduction is minimal among Hesperioidea and Papilionoidea. The prothoracic legs of both sexes are only slightly shorter than the mesothoracic and metathoracic legs and all "normal" parts of the tarsi and post-tarsi are present. To a slight degree, this is type 1 reduction.

In Lycaenoidea the females have the forelegs distinctly smaller than the mid- and hindlegs, but all five tarsal subsegments and the post-tarsus are present. The males not only have the forelegs quite small, but the post-tarsus is absent and some or all of the tarsal subsegments are fused. Thus females exhibit type 1 reduction while males have type 2 reduction.

Foreleg reduction is pronounced among Nymphaloidea, with marked miniaturization in both sexes. In males (Fig. 1) the post-tarsus is never present and, as a result of fusion, the tarsus superficially appears to have only one subsegment. In most nymphaloid families the female foreleg (Fig. 2), despite its minute size, retains all five tarsal subsegments and the post-tarsus, though the post-tarsal claws are absent in all but a few of the most primitive species. Again, type 2 reduction is found in males, type 1 in females.

Within each superfamily there is, of course, variation in leg ratios; this variation, which has useful taxonomic correlation, will be considered subsequently. Meanwhile, in order to illustrate



Figs. 1 and 2. Forelegs of *Vanessa atalanta*, coxae not shown, drawn to the same scale. Fig. 1, male; fig. 2, female. *Fm*, femur. *Pts*, post-tarsus. *PtsA*, post-tarsal apodeme (tendon). *Tb*, tibia. *Ts*, tarsus, with subscript numerals denoting subsegments.

in a general way the comparison among the four major taxa, the legs of both sexes of a typical species of each superfamily were measured and the pro- and methathoracic legs expressed as percentages of the length of the mesothoracic legs (Fig. 3).

The reduction of the forelegs of butterflies raises several interesting questions, one of which is that of selective value.

Many insects sacrifice ambulation in order to convert the forelegs to some other purpose having a clearly positive selective effect — mantids and mole crickets are among many possible examples. Such cases make it evident that the meso- and methathoracic legs suffice for ambulation; one may fairly assume that the forelegs can be altered and deprived of ambulatory function without *thereby* creating a negative selective effect. But may one properly conclude from this that the forelegs will actually be altered *unless* the alteration leads to a positive selective value? Certainly, there is no obvious selective advantage in the little forelegs of so many butterflies: is this a case of modification without either positive or negative selective value?

Apparently neutral, nonadaptive characters have been observed in animals and discussions to this point are found in most general books on evolution (e.g., Dodson, 1960: 250-251; Moody, 1953: 319, 328, 353-354). Dodson states that a character with truly neutral selective value can become established (1) through

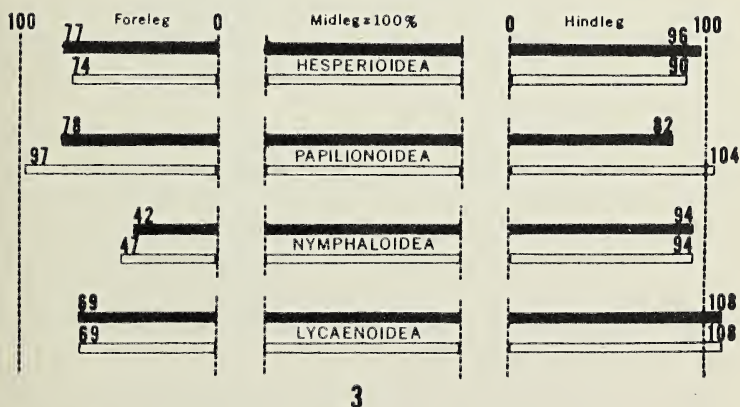


Fig. 3. Ratio of length of fore- and hindlegs to midlegs of four African species selected at random; measurements made from *Tagiades flesus* (Hesperiidae), *Papilio dardanus* (Papilionidae), *Cymothoe beckeri* (Nymphalidae) and *Iolais agnes* (Lycaenidae). Males shown by solid bars, females by open bars. Lengths of midlegs taken as unity.

genetic drift, (2) as an incidental effect of a pleotropic gene, (3) because of linkage with a beneficial gene, or (4) as part of the phenomenon of vestigiality. I have previously commented (Fox, 1956: 24-25) that the strongly aborted forelegs of Ithomiidae and related families might become established *merely* because foreleg reduction is not itself detrimental to survival for these insects.

But Dodson (1960: 250) makes the point that nonadaptivity is difficult to demonstrate and that many characters, which at first seemed to be selectively neutral, have proved upon closer analysis to have positive adaptive value. Are the little forelegs of nymphaloids really useless? Have they indeed only neutral selective value or is there some positive value?

It is most intriguing that the degree and type of foreleg reduction differs between the sexes in two of the four superfamilies. Why do the tarsal subsegments and the post-tarsus persist in females in spite of radical miniaturization, whereas in males with equally miniaturized forelegs, the post-tarsus and most of the tarsal subsegments are absent? Are forelegs more useful to female butterflies than to males? If so, what function can be carried out by a miniaturized foreleg but requires all the segmental components and cannot be performed by a leg having the tarsal subsegments drastically fused and reduced?

SUCROSE CHEMORECEPTION

Other than ambulation, the only important function ever demonstrated for butterfly legs is the perception of fluids — specifically, water and water solutions of sugars — by means of contact chemoreceptors on the tarsi.

Experiments reported by Minnich (1921, 1922a, 1922b), Weis (1930), Anderson (1932), Frings and Frings (1949, 1956), Kuwabara (1951, 1952, 1953), and Hodgson (1958) used the "Proboscis reaction" to demonstrate that butterflies perceive fluids via tarsi and proboscis. Individual specimens were restrained and the proboscis and legs were put into contact with various fluids; if the proboscis was extended as for drinking, perception was considered confirmed.

Most of this work was physiologically oriented and primarily concerned with finding the lowest concentration of sugar in water which would elicit the reaction. Several workers also sought a "negative" reaction to solutions of materials thought to be unpleasant to the butterfly. In general, little effort was made to discriminate among the pairs of legs as to respective perception.

Thus, sensitivity on the midtarsi was reported for papilionids, lycaenids and hesperids studied but there was no indication as to whether or not the fore- or hindtarsi were separately checked.

However, Minnich (1921) and Frings and Frings (1949, 1956) obtained selective data on all three pairs of legs for two pierids and six nymphaloids. The pierids studied both showed positive reaction to solutions via the ventral surfaces of the fore- and midtarsi but no reaction via the hindtarsi. The nymphaloids showed positive reaction via the mid- and hindtarsi but negative via the foretarsi. These results suggest a taxonomic correlation of considerable interest.

Reported results of experiments with butterflies along these lines are summarized in Table 1.

Eltringham (1933), apparently at Minnich's behest, prepared celloidin sections of the midtarsus of male *Vanessa atalanta* and reported the presence of trichoid sensilla scattered along the ven-

Table 1

Perception of Solutions by Contact Chemoreception
Recorded for Butterfly Tarsi

Family, genus & species	Reaction to solutions by			Reference
	Foretarsus	Midtarsus	Hindtarsus	
Papilionidae: <i>Papilio machaon</i>	?	+	?	4
<i>Papilio polyxenes</i>	?	+	?	4
<i>Papilio philenor</i>	?	+	?	5
<i>Papilio ajax</i>	?	+	?	2
Pieridae: <i>Colias philodice</i>	+	+	-	3
<i>Pieris rapae</i>	+	+	-	2, 3
Danaidae: <i>Danaus plexippus</i>	-	+	+	2, 3
Satyridae: <i>Lethe eurydice</i>	-	+	+	4
<i>Cercyonis pegala</i>	-	+	+	2, 4
Nymphalidae: <i>Limnitis arthemis</i>	-	+	+	4
<i>Limnitis archippus</i>	?	+	?	2
<i>Vanessa atalanta</i>	-	+	+	1, 2
<i>Nymphalis antiopa</i>	?	+	+	1
<i>Phyciodes tharos</i>	?	+	?	2
<i>Speyeria cybele</i>	-	+	+	4
Lycaenidae: <i>Lycaena thoe</i>	?	+	?	2
<i>Atlides halesus</i>	?	+	?	5
Hesperiidae: <i>Polites mystic</i>	?	+	?	2
<i>Epargyreus clarus</i>	?	+	?	5

+, positive reaction reported. -, negative reaction reported. ?, no observation reported. References: 1, Minnich, 1921. 2, Anderson, 1932. 3, Frings & Frings, 1949. 4, Frings & Frings, 1956. 5, Hodgson, 1958.

tral surface. He described these structures as "extremely slender, thin-walled tubes . . . set in sockets of the usual kind" and supplied with a trichogen cell, a tormogen cell and with "several sensory cells . . . having a distal process . . . which enters the delicate tube on the edge of its base, and taking a somewhat irregular course, extends right to the distal end, where there is a minute papilla." The setae were found to be about 150 micra long and 6.2 micra in diameter. Grabowski and Dethier (1954) examined the mid- and hindlegs of a hesperid (*Eupargyreus clarus*), a lycaenid (*Everes comyntas*), two pierids (*Colias eurytheme*, *Pieris rapae*) and a nymphalid (*Phyciodes tharos*) and found that "all possess on the tarsi only one type of thin-walled hair. This is blunt-tipped and usually curved, but the wall appears to be of equal thickness throughout." Foretarsi of females were not examined.

The supposition that these trichoid sensilla are the contact chemoreceptors concerned with detection of sugars and certain other solutions was confirmed by electrophysiological techniques by Morita and Takeda (1957, 1959), Morita, Doira, Takeda and Kuwabara (1957) and Takeda (1961).

Note that all reports on the morphology of tarsal chemoreceptors mentioned that these trichoid sensilla are scattered singly, and that no difference between the sexes — if, indeed, females were critically examined — was recorded.

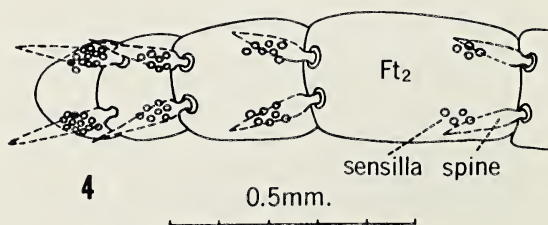


Fig. 4. Second (Ft_2), third, fourth and fifth foretarsal segments of *Speyeria cybele* female in ventral view to show arrangement of trichoid sensilla and spines.

CLUMPED SENSILLA ON FEMALE FORETARSI

Many years ago I noticed that the foretarsi of female ithomids bear clusters of translucent hairs on the ventral surface. More recently, while trying to find some sound morphological basis for recognizing species in *Mechanitis*, a genus in which male genitalia are valueless for the purpose, I made a comparative examination of the female foretarsi and noticed that these clustered hairs are in fact the setae of trichoid sensilla and that the clusters are always placed beneath the spine or spines borne on the preceding subsegment.

Since all available information indicates that sucrose sensitivity is not vested in the foretarsi of nymphalids, and since trichoid sensilla are known to be chemoreceptors, my curiosity was at once aroused. I then made whole mounts of the legs of several hundred butterflies representing all families and, of the Nymphaloidea, the principal subfamilies and tribes. Clustered trichoid sensilla were found on the foretarsi of all females of all groups, but such clusters were not found on foretarsi of males or on mid- or hindtarsi of any butterfly of either sex. (Details of the technique for whole mounts, which is quick, easy and permanent, are given in Cummins, Miller, Smith and Fox, 1965: 151-152.)

In order to verify the histological structure of these trichoid sensilla, legs were removed from freshly caught specimens of *Speyeria cybele*, fixed in Allen's modification of Bouin's fluid, embedded in high melting point (62°) wax, cut at 7 micra and stained for general examination with Mallory's triple stain.

On whole mounts of foretarsi of female nymphaloids, the trichoid sensilla (Figs. 4, 5, 6) are seen as groups of blunt-tipped,

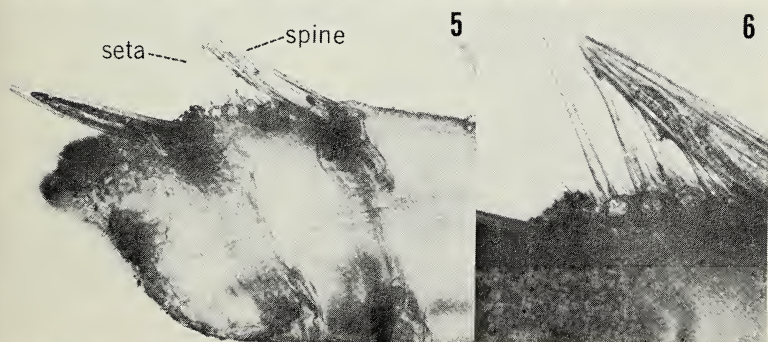


Fig. 5. Three terminal foretarsal subsegments of *S. cybele* female photographed in lateral view at 100x from a whole mount.

Fig. 6. Fourth foretarsal subsegment of same, photographed at 200x in lateral view.

translucent curved setae, each arising from the center of what appears to be a translucent disc or mound. These sensilla are arranged in tight clusters on the ventral side near the proximal end of a subsegment and beneath the ends of the large, prominent spines projecting from the distal end of the preceding subsegment. The number of sensilla in a cluster varies with the subsegment, the distal subsegments usually having the larger clusters; details of size, number and arrangement differ among various taxa.

In *Speyeria cybele* a pair of ventral spines arises at the distal margin of each of the first four foretarsal subsegments, one spine on each side of the ventral midline (Fig. 4). Beneath each spine there is a cluster of sensilla on the next distal subsegment; no such cluster is present on the first subsegment. The two clusters on the second subsegment each consists of four sensilla; on the third and fourth subsegments each cluster has seven sensilla; on the fifth subsegment each consists of twelve sensilla. The setae (Figs. 5, 6) are 72 to 98.4 micra long and 7.2 to 9.0 micra

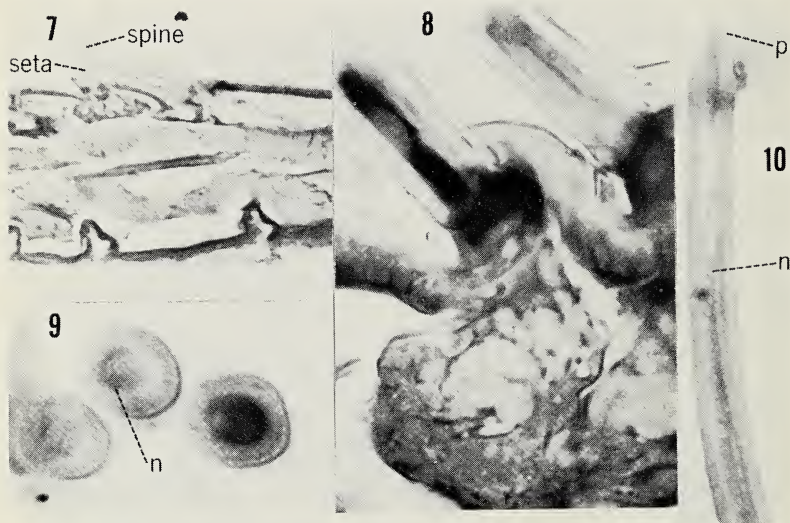


Fig. 7. Longitudinal section of foretarsus of *S. cybele* female, cut at 7 micra, stained with Mallory's triple stain and photographed at 100x, showing spine of first subsegment and two sensilla of second segment; only basal part of setae included.

Fig. 8. Same two setae and associated cells photographed at 1000x.

Fig. 9. Three setae in cross-section photographed at 1000x, showing position of dendrite (*n*) against wall of lumen.

Fig. 10. Longitudinal section through tip of seta photographed at 1000x, showing terminal papilla (*p*) and part of neural denrite (*n*).

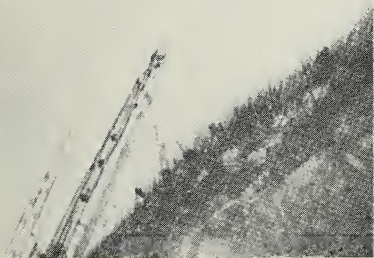
in diameter at the base. In each clump the setae appear to grade in length, the longest being distal. The discs or mounds in which the setae are 12.0 to 14.4 micra in diameter and are placed from 4.7 to 9.5 micra apart.

Examination of serial sections cut longitudinally (Figs. 7, 8) shows that each disc is a hemispherical mound set in a depression of the cuticular surface and that the whole structure is a trichoid sensillum much as presented by Eltringham (1933), Snodgrass (1935: 515-518) and Dethier (1963: pl. 11), with trichogen cells and, in this case, with apparently three neuron cell bodies. The setae are nearly round in cross-section, hollow, the walls about 1.75 micra thick (Fig. 9). The dendrites of the neurons (*n*) extend along the dorsal wall of the setal lumen to its tip, where there is a tiny terminal papilla (*p*) (Fig. 10).

As noted previously, Minnich (1921) and Frings and Frings (1949, 1956) showed that pierids studied differ from nymphalids studied in that sensitivity to sucrose solutions is present on the foretarsi of the former but not of the latter butterflies. In addition, therefore, to the clumped sensilla on the female foretarsus, pierids would be expected to have trichoid sensilla individually scattered along the foretarsi of both sexes. Whole mounts of the foretarsi of *Pieris rapae* confirm this situation.

Scattered along the entire ventral surfaces of the foretarsi of both sexes are trichoid sensilla separated from each other by at least 24 micra. Similarly arranged sensilla are found also on the midtarsi (Fig. 11) but not on the hindtarsi of both sexes.

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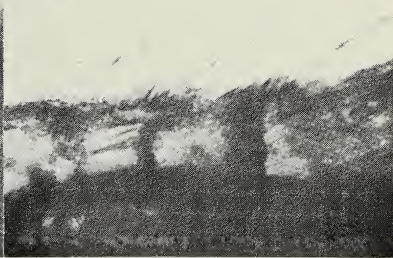


Fig. 11. Fifth midtarsal subsegment of *P. rapae* female photographed at 200x, showing ventral spines and scattered sensilla.

Fig. 12. Fifth foretarsal subsegment of *P. rapae* female photographed at 200x, showing clumped sensilla and paired spines.

Clumps of sensilla are present only on the foretarsi of females (Fig. 12). The discs are separated by 4.8 to 9.5 micra, otherwise these sensilla are structurally similar to the scattered sensilla. The setae are 55.2 to 60.0 micra long and 4 to 6 micra in diameter at the base. The two clumps on the fifth subsegment each consist of 12 sensilla, those on the fourth of four each and those on the third of two each; there are no clumps on the first or second subsegments.

The individually scattered sensilla are, as reported by Eltringham (1933) and others, the contact chemoreceptors apparently concerned with appreciations of solutions: confirmation has been provided by electrophysiological methods and there is correlation of structure and function. By the same token, the clumps of sensilla cannot be involved in detection of solutions, since these structures are present on the foretarsi of females shown not to possess on the foretarsi any sensitivity to fluids.

A clue to an additional foretarsal function in female butterflies was found in the work of Ilse (1937), who experimented with insect vision and color discrimination. She reported that ovipositing *Pieris brassicae* females, when placed on a green surface, reacted by rapidly drumming on the surface with the forelegs, but that no such reaction was elicited when the same females were placed on yellow or red surfaces. Ilse was content to interpret the drumming reaction as a sign that the butterfly recognized the color green, without wondering why recognition should be followed by such astonishing foreleg activity.

It occurred to me that the drumming reaction on the part of an ovipositing female might be an attempt by the butterfly to carry the visual recognition of green one step farther — the contact chemoreceptive identification of the correct larval foodplant.

As a crude preliminary investigation of this line of thought, ovipositing females of *Pieris rapae*, *Colias philodice*, *Phyciodes tharos*, *Speyeria cybele* and *Euphydryas phaeton* were netted in the field. Wings were clamped together with paper clips and the butterflies were placed on various colored surfaces. When black, white or orange surfaces were used, no reaction was observed. When a green surface was used, a form of the drumming reaction was observed in every case. The two species of pierids performed drumming exactly as Ilse described it for *P. brassicae*, a repeated, rapid alternating movement of the forelegs against the surface. In the three nymphalids the reaction consisted of a single darting motion, first with one, then with the other foreleg.

In all cases the terminal tarsal subsegments were brought into contact with and scraped along the surface at the end of the stroke.

Each female was then placed upon various green leaves, including the leaf of her foodplant. Each new offering was always drummed. Three females belonging to two species followed what apparently was the butterfly's recognition of her foodplant by oviposition: two different females of *P. tharos* laid eggs on leaves of aster but did not do so on other leaves offered; one female of *C. philodice* oviposited on a clover leaf but not on any other offering.

My theory — certainly not proved at this time — is that the female butterfly, by drumming, abrades with the tarsal spines the surface of the leaf, releasing essential oils and enabling her to detect via the clumped trichoid sensilla the material characteristic of the plant. It seems probable that, during my rough observations, the females who did *not* follow drumming on the larval foodplant by ovipositing were not ready to do so for other reasons or were inhibited by having the wings restrained. In any event, it does not necessarily follow that just because a female comes into contact with and recognizes her foodplant that she will immediately and invariably oviposit. On the other hand, the instances of ovipositing observed may have been mere coincidence and may have had nothing to do with drumming.

If, however, the above explanation of drumming turns out to be correct, the clumps of trichoid sensilla on the female foretarsi are also explained and the function which can be performed by miniaturized foreleg only if it is complete and unfused has been found.

Experiments are currently under way in our laboratory and are expected to shed additional light on these questions.

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A NEW SPECIES OF *EPINOTIA* HUBNER FROM BRITISH COLUMBIA (OLETHREUTIDAE)

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DURING THE PAST FEW YEARS an undescribed species of *Epinotia* Hbn. has been causing considerable injury by mining the leaves of the western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] in northern Vancouver Island, British Columbia. The description of it is presented here to enable officers of the Canada Department of Forestry to report on its injury and control.

***Epinotia tsugana* Freeman, new species**

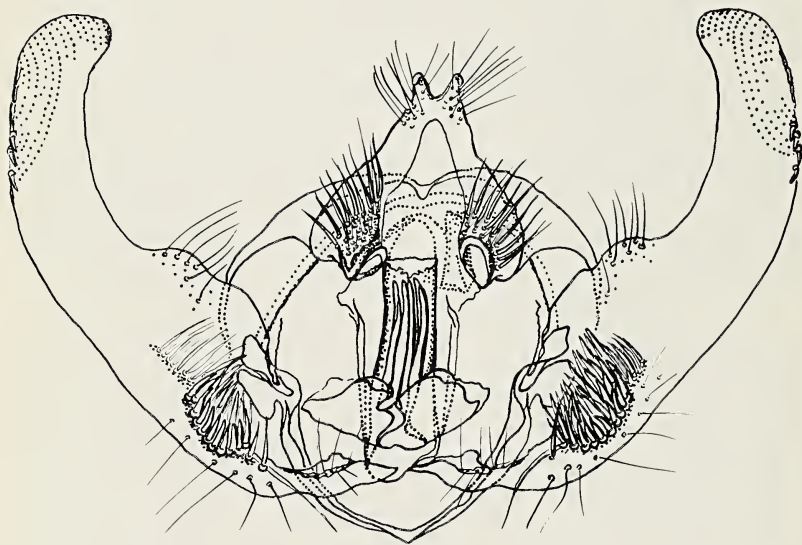
Colour and maculation. — Antenna grey with dark brown annulations. Palpus grey, darker apically. Head pale grey. Thorax grey. Forewing grey, sparsely covered with short, black, transverse dashes and light ochreous scales, more noticeable on the apical half; costal margin whitish, with evenly spaced, short transverse, black dashes; apical quarter with a transverse, metallic, leaden-grey bar from near the costa almost to the tornus; beyond with a subapical, curved, metallic, leaden-grey bar extending from the costa to the tornus; a narrow, black line extending around the apical margin; fringe grey, paler basally. Hind wing dark grey; fringe light grey, darker basally. Abdomen metallic leaden-grey. Legs grey; tarsi with black bands.

Wingspread. — 9.0-9.5 mm.

Male genitalia (Fig. 1). — Uncus well developed; bifid. Socii prominent; truncate at apex, Clasper arcuate; basal half much broader and with a cluster of short, thick spines near the base. Aedeagus short, stout, cylindrical; containing a cluster of six cornuti that are almost as long as the aedeagus.

Type material. — Holotype, male, Holberg, Vancouver Island, B.C., 13 May 1966. Type No. 7976 in the Canadian National Collection, Ottawa, Ontario. *Paratypes.* — Five males seven females, 2-20 May 1966; two females, 18 June 1965. All paratypes from Holberg, Vancouver Island, B. C. All type material reared from western hemlock by officers of the Canadian Forest Insect Survey, Canada Department of Forestry.

Remarks. — The maculation of *E. tsugana* somewhat resembles that of *Epinotia nanana* (Treit.). On the basis of the male genitalia however, *tsugana* is more closely allied to *Epinotia lomonana* (Kft.).



3

Fig. 1. Male genitalia of *Epinotia tsugana*.

STUDIES IN LIFE HISTORIES OF NORTH AMERICAN LEPIDOPTERA CALIFORNIA ANNAPHILA II¹

JOHN ADAMS COMSTOCK
and CHRISTOPHER HENNE

Del Mar, California and Pearblossom, California

IN CARRYING ON STUDIES of life histories of *Annaphilas*, prior to March 1964, a number of incomplete records and drawings were made which were withheld in the hope that additional information might be obtained. It now seems advisable to record these, as they may aid workers who are planning to publish more complete life histories.

***Annaphila astrologa* Barnes & McDunnough**

In our published notes prior to March 1964 we were unable to describe and illustrate the ovum of *Annaphila astrologa*. Later, eggs were obtained, and additional information recorded. Location of capture was the northeast rim of Bobs' Gap, Holcomb Ridge, Mojave Desert, Los Angeles County, elevation 4200 feet. The eggs were laid on *Emmenanthe penduliflora* Benth.

Egg: (Fig. 1 A)

Spherical, 0.5 mm. wide by 0.4 mm. tall.

Color, bright yellow. The surface is covered with 48 to 50 ridges, arising from the base and terminating near the micropylar depression. Several coalesce superiorly. Ridges are topped by a line of pearl-like nodules or expansions. They are closely crowded together, and there are apparently no cross lines between them. Eggs hatched April 9, 1964.

FIRST INSTAR LARVA: (One day after hatching)

Length, 2.5 mm.

Head width approx. 0.4 mm. Jet black.

The body is narrower than the head. It is cylindrical and translucent, and is tinged with light green from the first segment to about the eighth. The cauda is light yellow. The cervical shield is distinct, and is spotted with black. Legs, black. Prolegs, distally black.

SECOND INSTAR LARVA:

Head width 0.7 to 0.75 mm. Mottled yellow-green and black.

¹Illustrations reproduced from water color drawings
by

J. A. Comstock

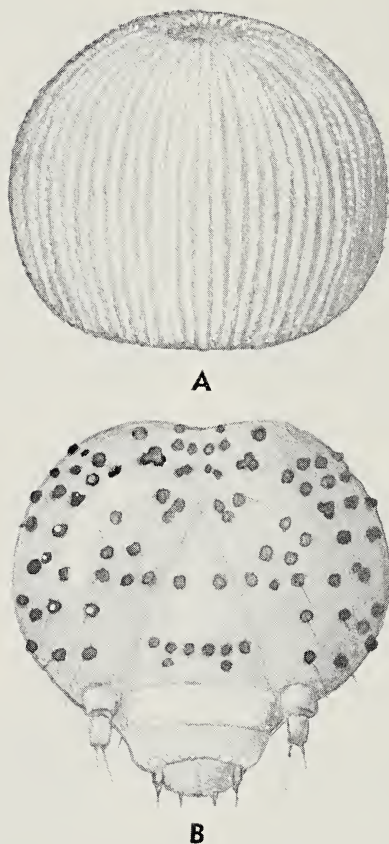


Fig. 1. *Annaphila astrologa* Barnes & McDunnough. A. Egg, enlarged X 95. B. Front view of head, enlarged.

Body, 7 mm. long. Color, deep green, with rows of small brown tubercles, each bearing a colorless seta. Legs tipped with black. Prolegs, yellow with brown crochets.

The third instar larva was described and illustrated in our prior paper (1964) but the distinctly marked and spotted head was reproduced on too small a scale to be clearly defined.

It is now pictured on Figure 1 B.

Head width is 1 mm. It is studded with numerous brown dots and blotches. Those which bear setae are raised. The ground color of the face is yellow with a tinge of green. The antennae and labrum are white.

Additional larvae were taken on the Mulholland Highway in the Santa Monica Mountains, May 16, 1965. The pupa illustrated in our prior paper (1964) was taken at Red Rover Canyon, southwest of Acton, Los Angeles County, elevation 3200 feet, May, 1963.

Larvae of all the *astrologa* complex produce their pupal chambers by cutting into pithy wood.

A colored figure of the moth was included by Draudt in Seitz, Vol. 7, 47e, 1927.

The type locality is Redington, Arizona.

REFERENCE

COMSTOCK, JOHN ADAMS and CHRISTOPHER HENNE, 1964. Studies in Life Histories of North American Lepidoptera. California Annaphilas. *J. Res. Lepid.* 3 (3): 175-191.

***Annaphila pseudoastrologa* Sala**

This species was published by Frank P. Sala in 1963. Prior to that he submitted a pupa under the manuscript name which we then illustrated and held for later verification.

In addition, we had taken larvae of the same species feeding on the flowers and buds of *Phacelia mincr* Thell, at Vasquez Rocks, Sierra Pelona Valley, Los Angeles County, April 1963.

There is still need of the ovum to complete the life history, but it is hoped that Sala will include this in his promised life history study.

LARVA, INTERMEDIATE STAGE: (Fig. 2 A)

Length, 8.5 mm. Head width, 1 mm.

Head is glistening light green, speckled with brown, heaviest over the crown. Ocelli, black. Mandibles edged with brown. Body, dark olive-green, with numerous raised white nodules, topped by relatively long setae. Middorsally, a narrow longitudinal white stripe, and dorso-laterally a similar stripe paralleling it. Below this, the body color gradually changes to a deep rose-purple, which extends downward to the spiracular line where it abruptly gives place to a deep green. This green also covers the entire venter. The spiracles stand on elevated nodules. They are black-centered with white circlets surrounded with rose-purple blotches. The caudal area has a considerable blotching of rose-purple, extending over the dorsum. The white setae

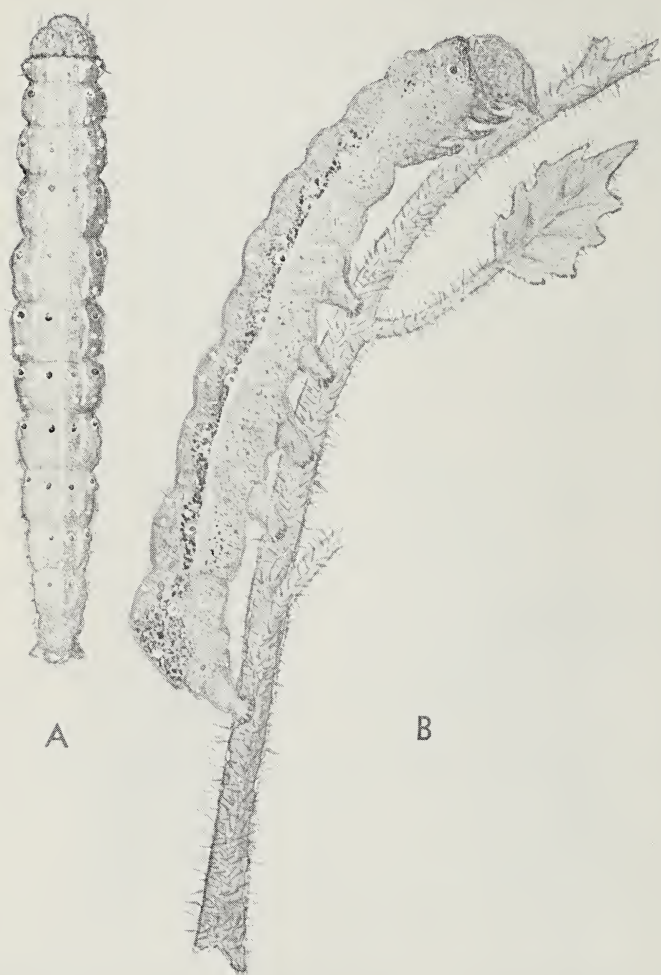


Fig. 2. *Annaphila pseudoastrologa* Sala. A. Larvae, intermediate instar, X 10. B. Mature larva approximately X 5.

are mounted on elevated nodules with black centers and white circlets. The legs and prolegs are green. Later, the rose-purple invades most of the dorsal surface.

MATURE LARVA: (Fig. 2 B)

Length, 20 mm. Width, through center, 3 mm. Head width, 2.1 mm. Head color is glistening light yellow, heavily sprinkled with light brown blotches and spots over the upper part of

cheeks and along the sides of the epicranial suture. The front is unspotted. Ocelli, dark brown, resting on yellow bases. Mandible, black. Setae, soiled white, arising from minute brown nodules.

First thoracic segment of body, yellow, with an orange cast, weakly mottled with light brown and white spots over dorsum, strongly blotched with brown laterally. There is a narrow middorsal white stripe. Remaining segments, basically yellow-green with thick spotting and mottling of darker green. As the spiracular area is approached, spotting changes to red-brown, with the black-centered and white-rimmed spiracles standing out in strong contrast. In caudal area, red-brown spotting extends over dorsum. There is a bare suggestion of a longitudinal middorsal stripe, formed by indistinct darker spots. Venter, unspotted light green. Legs, soiled yellow-green. Prolegs, mottled light green with brown crochets. All setae, relatively short and white, resting on small white papillae with minute black centers.

Prior to pupation the larva assumes a deep mottled purplish-brown color above the spiracular line, and the ventral green area becomes heavily mottled with purplish-brown and minute white dots. The stigmatal line becomes more pronounced and is lighter.

Thereafter the larva begins to chew its way into soft pithy bark, in which it weaves a pupal chamber.

In addition to *Phacelia minor* the food plant has been noted as *Phacelia parryi* Torrey.

PUPA: (Fig. 3 A, B, C.)

Length, 9.25 mm. Greatest width, 3 mm. Fusiform. Head rounded. Eyes relatively small. Maxillae terminate almost at the margin of the wing cases. Antennae, slightly shorter. Cremaster terminates in two short recurved spicules pointing laterally, and two minute spikes pointing caudally.

General body color, rich chestnut brown with lighter shade on the wings and abdominal segments. Antennae, nearly black. Wing cases, marked with an assemblage of buried black dots, predominating on forward half of wing, irregularly placed.

Body surface texture, predominantly finely rugose, but maxillae and leg cases bear fine raised striations. Other structural features are adequately shown in the illustration.

Our first pupa was obtained in 1956 from Frank Sala. It was collected in Latego Canyon above Seminole Hot Springs, Los

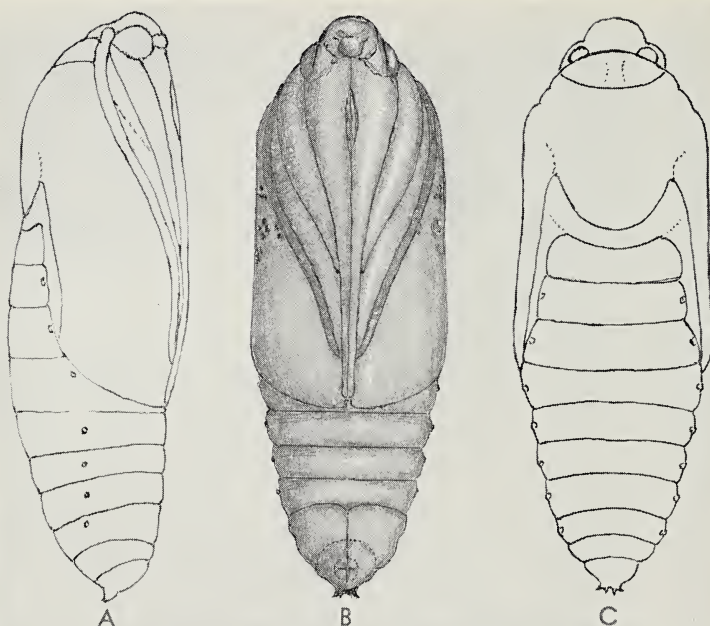


Fig. 3. *Annaphila pseudoastrologa* Sala. Pupa, A. lateral, B. ventral, and C, dorsal aspect, approxim. X 7.

Angeles County, which its author later designated the type locality. The moth is pictured on pages 290 and 292 of Sala's original 1963 description.

REFERENCE

SALA, FRANK P.

1963. The *Annaphila astrologa* Complex, with Description of Three New Species. Jour. Res. on the Lepid. 2 (4): 289-300.

Annaphila vivianae Sala

This species was published by Frank Sala in 1963. Prior to that (1956) he sent us pupae with his manuscript name "*vivianae*" attached, which made possible the description and drawings presented here.

PUPA: (Fig. 4 A,B,C)

Length, 9.5 mm. Greatest width, 3 mm.

Body color, dark reddish-brown. Wings, lighter. Spiracles, dark brown.

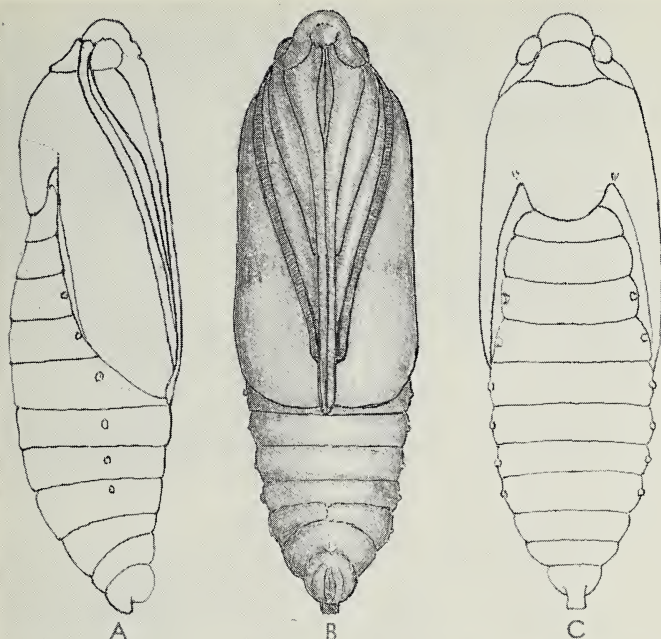


Fig. 4. *Annaphila viviana* Sala. Pupa, A. lateral, B. ventral, and C, dorsal aspect, approxim. X 7.

The antennae terminate 0.8 mm. cephalad to the wing margins, and the maxillae extend slightly beyond these margins. The head is rounded and the eyes not prominent. The spiracles are slightly elevated. The cremaster is a rounded knob with a squared plate extension devoid of hooklets. Other structural features are shown in the illustration.

The range of the species is the southern Sierra Nevada Mts. Type locality, the Lower Kern River Canyon, Kern County, California. It also extends north to Three Rivers and the East Kaweah River, Tulare County. It may in addition be found throughout the range of its specific food plant, *Phacelia cicutaria* Greene, among the rocky out-croppings in the foothills of the Sierra Nevadas, from Butte County south to the Tehachapi Mountains. An additional foodplant successfully used in the laboratory was *Phacelia tanacetifolia* Benth.

REFERENCE

SALA, FRANK P.

1963. The *Annaphila astrologa* Complex with Descriptions of Three New Species. Jour. Res. Lepid. 2 (4): 289-300.

Annaphila diva Grote

This species was briefly discussed in our 1954 paper. We recently secured a mature larva, pupa, and cocoon which makes possible an illustration and a few additional notes concerning its life history.

Our larva was preparing for pupation, which may account for its somewhat darker color and foreshortening in form as compared with William H. Evans' description in the Rindge and Smith 1952 Revision of the Genus.

MATURE LARVA: (Fig. 5 A and B)

Length, 19 mm. Greatest width through center, 3 mm. Head width, 1.9 mm.

Head (Fig. 5 C) ground color, glistening soiled yellow, blotched with black, particularly over the crown. Ocelli, black. Antennae, white at base, dark on distal two-thirds. Margins of mandibles, black.

Body, predominantly striped and blotched with black, interrupted with various light lines and spots. There is a middorsal longitudinal line of dull pink, lighter on the anterior segments, gradually darkening toward the cauda. Lateral to this is a wide gray area. On the margin of this is a distinct light pinkish band running from the first to third segment. Beyond this is a wide band of mottled black running caudally, and extending downward to the wide spiracular band. This band is dull pink or pinkish-white, and it runs the entire length of the body. The black spiracles are located close to its upper margin. Several round light spots and a few irregular larger blotches occur on the body as shown on the illustration.

The cocoon was composed of soil granules. In shape it was oval — length, 10 mm. Width, 5.6 mm.

PUPA: (Fig. 5 D)

Length, 8 mm. Greatest width through center, 2.75 mm. Color throughout, uniform dull orange. Texture, glistening.

The maxillae reach to the wing margins, and the antennae are slightly shorter. The wing covers are translucent, allowing the segmental junctures to be dimly seen through them. The caudal segment is evenly rounded, and bears no spines or cremasteric hooks.

The species ranges from southern California to British Columbia.

The larval food plant is *Montia perfoliata* (Donn) Howell, and the adults have been taken in association with other species of *Montia* throughout its range.

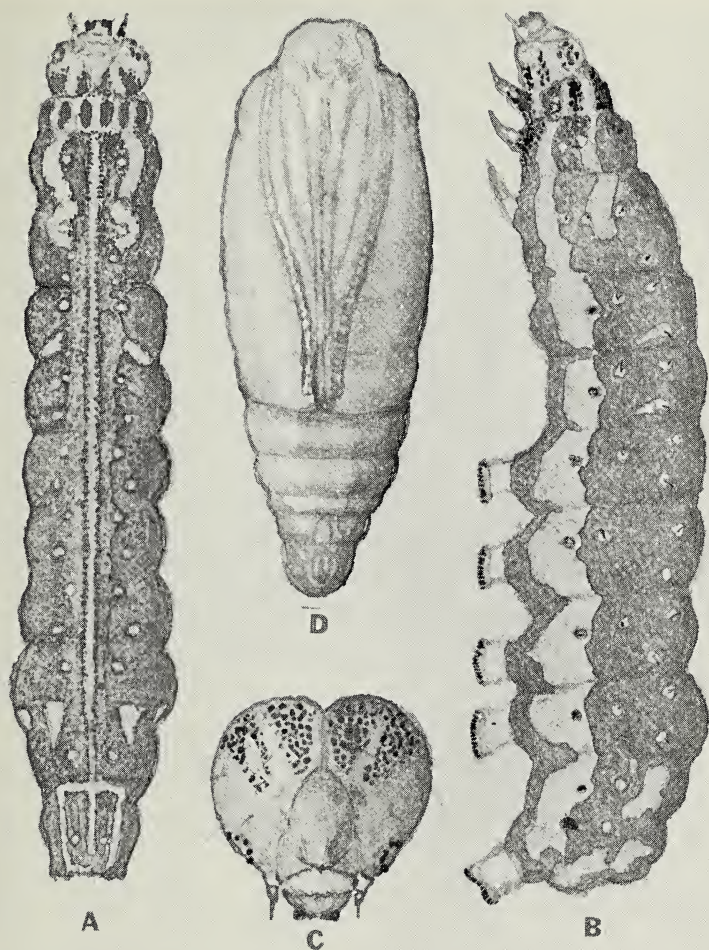


Fig. 5. *Annaphila diva* Grote. Mature larva, A. dorsal, and B. lateral aspects, X approx. 5. Head of larva, C, X 10. Pupa, D. ventral aspect, X approx. 8.

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***Annaphila spila* Rindge and Smith**

Females of this species were observed ovipositing deep in the flower bracts of *Linanthus montanus* Greene, in a meadow off Mineral King Road, East Fork Kaweah River, Tulare County, California on May 3, 1963 at an elevation of 3200 feet. Females were also confined from this locality and oviposited readily on growing plants transplanted from the field to the laboratory.

EGG: (Fig. 6 A)

Nearly spherical, slightly flattened at the base. Diameter, 0.4 mm. There are from 30 to 32 ridges running from base toward micropyle. These are knobbed along their crests. The ridges are slightly wavy and their knobbed crests are not uniform in size or direction. The grooves between the vertical ridges show minute and barely visible horizontal striae.

The micropylar depression is large and deep.

Color, bright orange, turning to riddish prior to hatching.

FIRST INSTAR LARVA: (A single example, observed May 21, 1963)

Length, 2.75 mm. Head width, 0.25 mm.

Head, jet black. Body, rich yellow with a tinge of orange. First thoracic segment with a shading of brown, due to minute dots forming a prothoracic shield. There is similar shading on the last caudal segment. There are minute dark dots on the dorsal area, some of them probably giving rise to colorless setae. Legs, shading to black at the tips. Prolegs, concolorous with the body. With only a single larva for observation, unusual care in handling was necessary, so some details were likely not noted. In spite of precaution the larva died.

The early instar larvae feed within the bracts and consume the buds of the young plants. They are not readily seen in the field at this stage. The adult larva rests upon the reddish stem of the food plant, feeding externally upon the flowers and buds, its coloration blending with that of the plant.

MATURE LARVA: (Fig. 6 B)

A single example was obtained June 13, 1963.

Length, 13 mm. Width through 9th segment, 2 mm, Width of head, 1.4 mm.

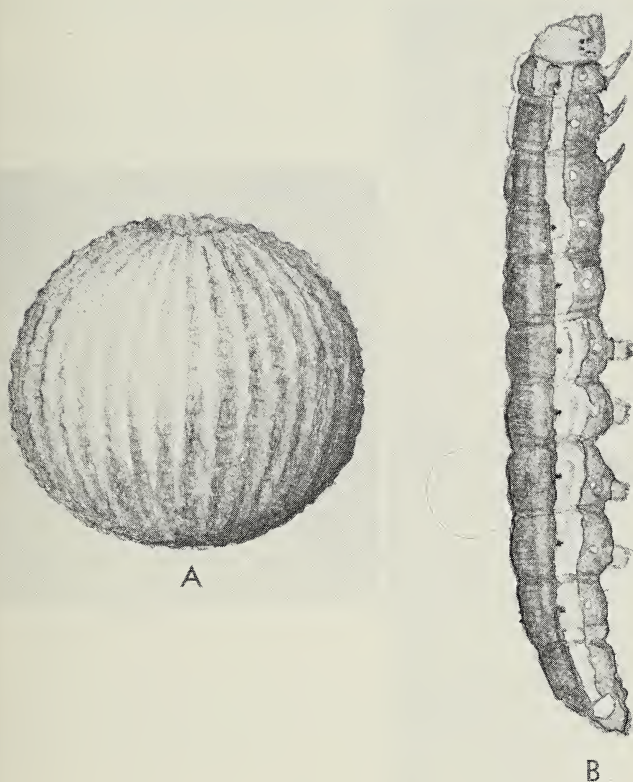


Fig. 6. *Annaphila spila* Rindge & Smith. Egg. A. approx. X 100. B. Larva, X 12.

Head, clear glistening yellow, the mouth parts slightly darker. Ocelli, black.

Dorsal half of body, deep pinkish-rose. The first segment has a middorsal yellow line extending slightly onto the 2nd segment. There is also a short dorso-lateral line on the 1st segment only. A wide stigmatal cream-colored band runs the entire length of the body. The spiracles are placed on its upper edge. Below this spiracular band the body is pinkish-rose as is also the venter. In

the middle of the venter the rose color becomes gradually lighter, with a suggestion of yellow. Spiracles, small and dark-centered, with a faintly suggested white margin below each one. Legs, translucent yellow, with dark tips. Prolegs, pinkish-rose, except for those on the head and cauda.

Our few examples failed to pupate as the flowers of the *Linanthus* became too dry for the larvae to feed upon and substitute food plants (other species of (*Linanthus*) proved unsuccessful.

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NEW SKIPPER RECORDS FOR MEXICO

H. A. FREEMAN¹

Garland, Texas

DURING THE PROCESS of making a careful systematic study of the HesperIIDae of Mexico my attention was drawn to three species of skippers located in specimens obtained from Dr. T. Escalante, Mexico, D. F., and one species in material recieved from Stallings & Turner, for determination. As there are no published records of the occurrence of any of these four species from Mexico I am recording them as new records for that country.

Astraptes helen Evans

This species was described as a subspecies of *parisi* Williams by Evans, the basic difference being in the genitalia. In this group of *Astraptes* there are several sibling species which are actually best separated by their genitalia, indicating that we should consider *helen* and *parisi* as separate species since their genitalia differ considerably. *A. helen* was described from San Pedro Sula, Honduras. Besides the seven specimens in the British Museum from Honduras, Evans also records Nicaragua and Panama as constituting the range of that species based on material available to him.

Among the specimens received from Dr. T. Escalante for study was found a male *helen* from Paraje Nuevo, Veracruz, Mexico, IV-52. This constitutes a new hesperiid record for Mexico.

Cogia mala Evans

This species was described by Evans from two males collected in Guatemala during 1904 by A. Hall. From what information available there are no other records for this species.

Among Dr. Escalante's specimens was found a male *mala* from Acahuizotla, Gro., IX-60. While collecting just north of Tehuacan, Pue., August 15, 1964, I collected five males of this species. This is another new record for Mexico. It was interesting to note that *Cogia aventinus* Godman & Salvin was found in the Escalante material from Acahuizotla also. *Mala* and *aventinus* show considerable superficial relationship, however, the larger hyaline

¹This research has been made possible by a research grant GB-4122 from the National Science Foundation for which I am deeply thankful.

spots of *mala* and the difference in the genitalia make these two species easy to separate.

Ouleus cyrna (Mabille)

This species was described by Mabille from a female, collected in Chiriqui, Panama. Later it was redescribed by Godman & Salvin as *simplex* and then *fasciata* from material collected in the same general area as the Mabille specimen. Evans records *cyrna* from Costa Rica and Panama, based on specimens in the British Museum. In the Escalante HesperIIDae there was found a female *cyrna* which had been collected at Sta. Rosa, Comitán, Chis., Mexico, IX-63. This is the first time that this species has been recorded from Mexico.

Carystoides lila Evans

This species was described from L. Sapatoza Region, Chirigua district, Columbia. Evans records it from Honduras, Columbia, Venezuela, and Ecuador. Stallings & Turner collected a female (which is in my collection) *lila* at Tamazunchale, S. L. P., Mexico, VI-6-41. Apparently this is the first record for this species from Mexico.

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A MOTH SHEET

FOR ATTRACTING AND RETAINING LIVE SPECIMENS
WITHOUT THE USE OF A TRAP OR TENT-ENCLOSURE.

NOEL McFARLAND

South Australian Museum, Adelaide, South Australia

FOR MANY COLLECTORS who have no need or desire to trap and kill the vast numbers of insects coming to their insect-attracting lights, the type of device described below is very much worth the trouble to construct. It is — in any event — useful, as it effectively increases the power of the sheet-and-light combination to draw in, and “hold”, nocturnal flying insects. It is of particular value to entomologists who are interested in capturing live females, for purposes of obtaining eggs for rearing and life history investigation. This “PARABOLIC MOTH-SHEET” was in constant use, along with several “conventional” set-ups (flat sheets with lights hanging in front of them) for a continuous period of 20 months in a single locality (McDonald Forest, 5 miles west of Corvallis, Benton County, Oregon; October 1961 to June 1963). I constructed it at the suggestion of Mr. Gerald Benedetti, then a graduate student in Mechanical Engineering at Oregon State University.

The effect of directing a correctly-located light at a vertical sheet, which is *held in the shape of a parabolic curve*, is such that the whole reflecting-surface (i.e., the whole sheet) appears to be the source of the light.. This results in a very different situation from that observed in the usual (flat) sheet-and-light combination, where there is a circle of fairly intense light at the middle of the sheet only. When the sheet is bent in the form of a parabolic curve, the whole sheet appears to “come alive” with the brilliance of the light it is reflecting, provided that the light is placed at the correct distance from the (inside) vertex of the curve. The distance of the light from the vertex is determined by the shape of the parabolic curve in use; see Fig. 1 (A-D) and photographs.

The size of the sheet (or canvas) used during the trial-period in western Oregon was 16 feet x 7 feet, and it was in operation at ground level, being held in position by 13 vertical poles run-

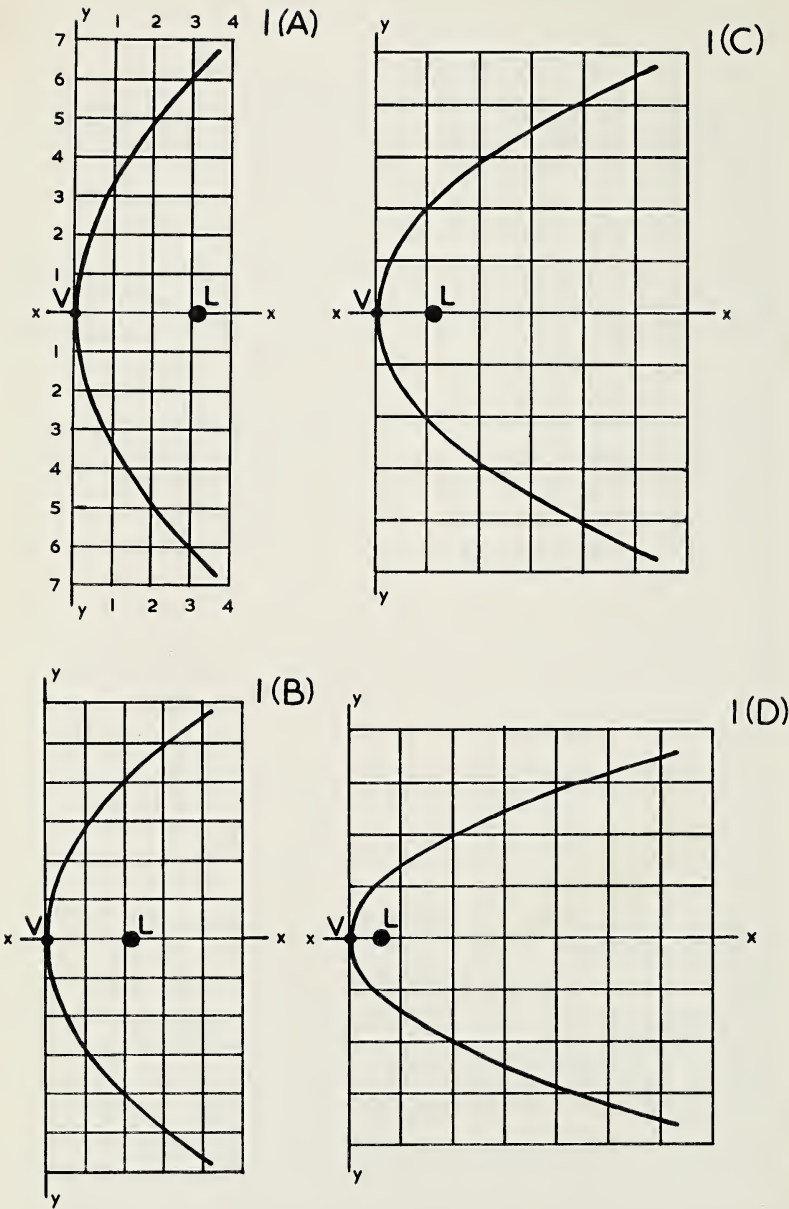


Fig. 1 (A-D) —Diagrams of four possible curves for the Parabolic Moth Sheet. Light source at (L), on a vertical pole. Vertex of curve at (V). Squares are one foot square. Sheet is 16 feet long, shown as if viewed from directly above .

ning through sleeves which were sewn to the canvas; the poles were in turn inserted into short ground-stakes (see Fig. 2) which were easily hammered into the ground. The placement of these ground-staks determined the accuracy of the resulting parabolic curve made by the canvas. Guy wires from the tops of the poles secured the whole structure in the event of high winds. Two 18-inch, 15-watt black light tubes (G.E. F15T8/BL) were hung vertically on the light-pole, one facing directly at the inside vertex of the curve, and the other facing in the opposite direction. (The addition of this second, outward-directed light did not seem to affect the results greatly, although it may have increased the "attracting-power" of the device). The general appearance of the whole set-up can be seen in the photographs, which are of the original parabolic sheet used in Western Oregon.

There are various ways and materials for constructing such an apparatus, either with the intention of making it portable (as described above), or heavier and permanent in one location. The important points are to maintain the parabolic curve with reasonable accuracy, so that the entire sheet appears to be throwing out the light, and not to make the sheet too small. The more surface area for incoming moths to land upon, the better. The 16 foot x 7 foot canvas operated in Oregon did a very impressive job. Of six black light and sheet set-ups in use in the one locality, the parabolic (curved) sheet invariably drew in, and retained, far more insects than any of the others; usually it had a greater catch than the totals of the other five combined.

Moths coming to the parabolic sheet have a greater tendency to remain and settle there. They often bounce back and forth within the curving enclosure before finally settling, but there is not much loss from individuals simply flying off around either end, or over the top, and not returning. (This is one of the disadvantages of a conventional flat sheet operating without any sort of trapping device). Some of the moths will fly around to the unlighted back of the sheet (the outside of the curve) and settle there; it is highly desirable to leave the back unlighted to accommodate such moths, as these are the individuals that would sometimes settle in nearby vegetation after once flying to the light; such species — this is sometimes a behavioral difference between species — are usually missed or overlooked at conventional flat sheets. When this occurs it often pays to shake or lightly beat nearby vegetation, which will cause many of the moths to fly back to the sheet, unless it

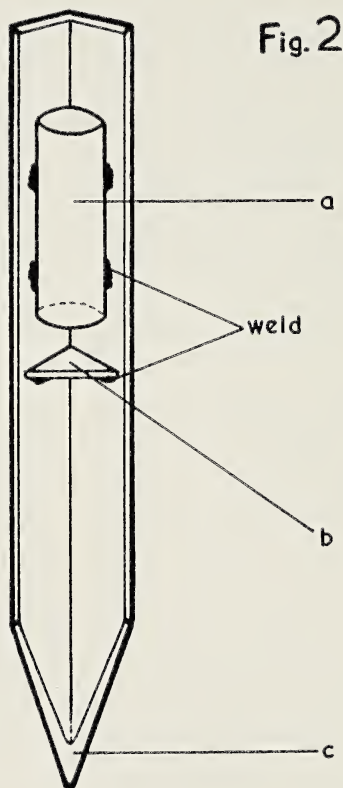


Fig. 2 — Diagram of a Ground Stake, which is easily pounded into the ground to receive the poles that will form the parabolic curve of the sheet. Made of $1\frac{1}{2}$ -inch angle iron. Total length about 21 inches. a = 6-inch metal tube, welded into angle iron 3 inches below the top; this tubing is a fraction larger than the diameter of the pole it is to receive; b = a small triangular plate of iron, welded about one inch below the bottom of the tubing, to stop the pole at a specified height after it is inserted through the tubing; c = tapered point on angle iron makes it easier to drive into hard ground.

is cold, in which case most of them will just drop to the ground.

There are many different parabolic curves that could be tried, and some may prove to be more efficient than others in "holding" the moths on the sheet; perhaps also in drawing them to the sheet in the first place. Four possible curves to try are suggested in Fig. 1 (A-D). All comments in this paper are based on experiences with only one of those parabolic curves (Fig. 1A), the shape of which is determined by the light source being set at three feet from the inside vertex of the curve. The light

faces directly toward the inside vertex of the curve, as it hangs on a vertical pole which is set at the specified distance out from the inside vertex of the curve. In my experiments, using the curve shown in Fig. 1A, two lights were in operation — one facing the vertex, and the other on the opposite side of the light-pole, facing directly away from the vertex. Other placements of the light (or of several lights) on the pole could be tried, and these might give varying results.

For spacing all the poles correctly on the ground, the easiest method is to stake out 2 strings at right angles to each other, along the ground, one representing the x-x axis (8 feet long is sufficient), and one representing the y-y axis (16 feet long is sufficient). Measurements are made by going out from the vertex, on the x-x axis, and then going either up or down parallel to the y-y axis, to the correct measured distance, for placement of each pair of corresponding opposite poles. (The only single pole, not having an opposite, is the one at the vertex). The sheet should be stretched tightly, so that the end result presents a smooth, wrinkle-free, evenly-curving reflective surface. A soiled, "off-white" canvas or sheet is preferable to a pure white one, for purposes of getting the moths to settle on the sheet with a minimum of flying about. A ground-sheet ("apron") is very desirable along the bottom of the curve. This can be made in 4 four-foot sections, which are easily snapped on along the bottom of the curve after it is set up. (If it is all in one piece, there are too many wrinkles in a 16-foot curving piece). An advantage in having the apron detachable is that it may be removed and washed from time to time, without the inconvenience of taking down the whole structure. After one wet season on muddy ground, the apron becomes the color of the soil, in which case it is rendered practically useless until it is washed. To be of much value, the apron should extend out onto the ground, from the base of the curve, for at least 18 inches all the way around. It is not needed on the back (outside) of the curve.

If a few pieces of curved bark (as available) are placed on the ground around the sheet, it will be found that certain moths (often of the same species) will hide under these, rather than disappearing into nearby weeds or ground litter; in this category are certain noctuids such as some *Agrotis*, *Euxoa*, and *Ufeus* spp., among others. Quite a few moths will settle on the guy wires, especially (for some unexplained reason) on cold nights; thus the guy wires should be rope or cord, not a smooth-surfaced



material. These and other refinements can be included to suit the intentions of the collector.

To experiment with other parabolic curves for the sheet (i.e., where the light is at some distance from the vertex other than the examples illustrated by Fig. 1.) the following general equation, for determining any points on a proposed parabolic curve, can be used: $y^2 = 4 AP$. We are solving for P, which is a point on the proposed parabolic curve, when y is a known distance up or down the y-y axis from its intersection (V) with the x-x axis, and A is a KNOWN distance of the light source (L) from the vertex (V), along the x-x axis. This is plotted on graph paper. Lay out the y-y axis and the x-x axis on the graph. When the curve is drawn in, it is to be symmetrical about the V-x axis, with its vertex touching V.

An example follows, to show the steps in finding a point on the proposed curve, when y is set (for example) at 6 feet up or down from the vertex, along the y-y axis, and the distance (A) of light source to vertex is set at 3 feet:

$$y^2 = 4 AP \text{ (solving for P)}$$

$$12 P = 36$$

$$P = 3 \text{ feet}$$

In other words, a point on the proposed curve, either 6 feet above or below the x-x axis, is located 3 feet to the right of the y-y axis.

Repeat similar calculations again for several other points on the same proposed curve, setting y at, say, 1, 2, 3, 4, 5, and 8 feet, and keeping the distance (A) of light source to vertex the same in each calculation. Place appropriate dots on the graph after each calculation; when finished, the series of dots may then be connected, resulting in the desired parabolic curve. Using graph paper divided into $\frac{1}{2}$ -inch or $\frac{1}{4}$ -inch squares, it is only necessary to solve for about 6 or 7 points on a curve that is to be in the vicinity of 16 feet long. This will give a curve sufficiently accurate to produce the results described above. Anything more precise is not practical to attempt setting up (or to maintain) under field conditions.

ACKNOWLEDGMENTS

I am indebted to Mr. Gerald Benedetti of Livermore, California, for the original suggestion of trying a parabolic curve, and for plotting the curve that was used; to Mr. Lloyd M. Martin of

the Los Angeles County Museum, California, for many helpful suggestions on the construction of various types of portable collecting sheets, frames, and ground stakes.

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COVER PHOTO

Daritis ? howardi Hy. Edw.

(PERICOPIDAE)

Penultimate instar, filled-out, resting on *Eupatorium* stem.
(Length: 80 mm. when filled-out in final instar).

Collected at approx. 7200 ft. elev., on the W. slope of Cabezon Peak, Sandoval Co., NEW MEXICO; 11 OCT. 1958 (half grown); S. L. VanLandingham, collector; on *Brickellia* sp.(?)

Reared to the pupal stage by Noel McFarland, on a substitute plant, *Eupatorium rugosum*, in Lawrence, Kansas.

Color transparencies by Carl W. Rettenmeyer.

Larva should be hanging from the branch rather than standing upright.

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REDISCOVERY OF *ANNAPHILA CASTA* HY. EDW. IN CALIFORNIA (NOCTUIDAE)

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AFTER THE PREPARATION of the manuscript dealing with a re-evaluation of *Annaphila casta* (Buckett, 1965), more specimens have become available for study. In addition to the two California specimens cited by Rindge and Smith (1952), there are now a number more California specimens available. In the author's and Mr. Bauer's joint private collection, there are 3 males and 12 females that were collected in central California; all the specimens are in good to excellent condition.

During the autumn of 1964, Mr. Noel LaDue of Sacramento brought some diurnal moths to Mr. Bauer, and eventually to me also, for determination. Much to our astonishment, some of the moths were the very scarce, and long sought *A. casta*. The specimens were collected earlier the same year on 10 May, near Plantation, Sonoma County, California. During the following spring of 1965, Mr. Bauer, Mr. M. R. Gardner and I made several attempts to collect *A. casta* near Plantation, but failed on our earlier attempts. It was not until the exact date of 10 May, 1965 that Mr. Bauer, Mr. LaDue, and I succeeded in collecting specimens of *A. casta*. Subsequent collecting expeditions were made, one on the 12th of May and another a week later; however, no specimens of *A. casta* were taken, or even seen.

It seems rather odd that the species is apparently so restricted in its period of flight! Yet the same trend was observed in the spring of 1966. It was very difficult to determine just where the specimens were coming from, and therefore it was equally difficult to locate a probable larval host plant. The specimens collected on 10 May 1965 were observed floating from the skies between the upper canopies of the redwoods (*Sequoia sempervirens* Endl.), to alight in a meadow during the morning rays of the sun.

Their actions were typical of species within the genus, especially the slow waving up and down of the wings while the specimen was alighted. There was apparently no particular preferred

alighting spot, as specimens were taken from the ground, grass, and low growing young redwoods. During the spring of 1965, little attempt was made to determine the larval host plant(s) of *casta*. During 1966, however, Mr. and Mrs. Chris Henne were in the vicinity of Plantation, and ardent attempts were made to determine a larval host plant relationship, but with no positive results. To date there is apparently no knowledge as to the larval host plant(s) of *A. casta*.

While collecting *A. casta* during 1965, it was noticed that the moth occurred only in one very limited area. Other adjacent areas with virtually the same environment as this one particular meadow yielded absolutely nothing, nor were any specimens of *casta* even seen. As yet, there is no explanation for this acute endemism, although it is believed with additional biological information gained in relation to *casta*, a logical hypothesis might result.

Buckettt (op. cit.) discussed various possibilities for the correct type locality of *A. casta*. It was (and still is) believed that the type locality of the species is in Oregon, not in California (for evidence to support this idea, refer to the aforementioned paper). One fact that is supported by the recent collections of *casta* is the probable validity of the labels on the two specimens contained in the American Museum of Natural History in New York City. These two specimens are labeled: "Sonoma Co. May Cal." and "Sonoma Co. May Calif.," and because they are each labeled differently there is the suggestion that the specimens were probably collected during different years. Judging from the evidence available in the literature, the Oregon type locality, in all probability is the correct one.

It is hoped that in the future more work will be done in attempting to solve the life history of *A. casta*. Also, it would be of academic interest to determine whether or not *casta* has a continuous vs. discontinuous distribution between its known localities (namely Sonoma and Mendocino Counties, California, and Benton and Douglas Counties, Oregon). I would like to extend my appreciation to those individuals that took part in this project: Mr. Bill Bauer; Mr. Mike Gardner; Mr. and Mrs. Chris Henne; Mr. Noel LaDue.

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STUDIES ON THE NEARCTIC *EUCHLOE*

PART 1. INTRODUCTION

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THIS PAPER WILL SERVE as the introduction for a series of papers which will present the results of an investigation primarily concerned with systematic placement of Nearctic members of the genus *Euchloe* Hübner. The genus *Euchloe* is composed of butterflies known as "marbles" which are members of the family Pieridae. The larvae of these insects feed upon species of Cruciferae. Populations of one or more species are found throughout most of the Nearctic Zoogeographic Region but occur most frequently in somewhat xeric habitats in the western United States and Canada. The taxonomic relationships of the Palaearctic and Ethiopian members of the genus are not considered in this study. Brief references will be made to the Old World entities in order to clarify important points relating to Nearctic members of the genus.

The author hopes to correct several faulty systematic concepts which have been applied to the Nearctic members of *Euchloe* for many years. These misunderstandings were due to the fact that the adults were identified by a few superficial external characteristics.

To correct the above stated situation, an attempt has been made to arrive at a more meaningful systematic treatment of the genus which will reflect probable phylogenetic relationships. This study presents the results of an analysis based on morphological, distributional, and ecological characteristics of all Nearctic members of the genus. Based on this analysis a workable systematic framework is presented.

Four species of Nearctic *Euchloe* are recognized: *E. ausonides* (Lucas), *E. creusa* (Doubleday), *E. olympia* (Edwards), and *E. hyantis* (Edwards). These are believed to be phylogenetically and morphologically divisible into two species groups. One is comprised of *E. ausonides*, *E. creusa* and *E. olympia*, and will be referred to as the *E. ausonides* group. The other is composed of *E. hyantis* and its several segregates; this group will be referred to as the *E. hyantis* complex.

¹The bulk of the material presented in this series of papers was part of a thesis presented in partial fulfillment of the requirements for the degree of Master of Arts at San Jose State College, San Jose, California. Dr. J. W. Tilden of the above institution was research advisor.

Two new combinations will be presented as subspecific designations of *E. hyantis* in a later paper.

Below are the titles of the papers which are anticipated for this series.

Part 1: INTRODUCTION

Part 2: CHRONOLOGICAL LITERATURE REVIEW
AND BIBLIOGRAPHY

Part 3: COMPLETE SYNONYMICAL TREATMENT

Part 4: TYPE INFORMATION

Part 5 DISTRIBUTION

Part 6: ADULT MORPHOLOGY AND KEY TO IDENTIFICATION

Part 7: LARVAL MORPHOLOGY AND KEY TO IDENTIFICATION

Part 8: BIONOMICS

Part 9: DISCUSSION AND SUMMARY

ACKNOWLEDGMENTS

The author expresses his gratitude to J. W. Tilden of San Jose State College who gave direction to this study. F. M. Brown, H. K. Clench, C. F. dos Passos, Paddy McHenry, J. A. Powell, and N. D. Riley contributed advice and information which made the construction of the synonymies and the writing of the portions which dealt with the type material an easy task. P. R. Ehrlich, T. H. Emmel, C. L. Remington, O. E. Sette, and Fred Thorne contributed invaluable information on the biology and the morphology of the genus. A. B. Klots, C. D. MacNeill, L. M. Martin, as well as Tilden gave freely of their knowledge on biological concepts with special regard to members of the genus *Euchloe*. I am also grateful for the advice on special techniques, equipment, and methods which was given by R. C. Ballard, J. G. Edwards, W. E. Ferguson, C. D. MacNeill, J. A. Powell, C. L. Remington, and J. W. Tilden. I greatly appreciated the suggestions of Leroy Parks, E. S. Ross, and Ronald Stecker about details concerning the format of these papers. My sincere thanks to Peter Herlan, Nevada State Museum, MacNeill, California Academy of Sciences, Martin, Los Angeles County Museum, Powell, California Insect Survey, University of California, Berkeley, and F. H. Rindge, American Museum of Natural History who allowed me to examine or borrow the specimens of *Euchloe* in collections under their care. The following individuals kindly loaned specimens from their personal collections: Richard Brown, Concord, California, John Lane, Los Angeles, California, R. L. Langston, Kensington, California, R. E. Stanford, Los Angeles, California, and Fred Thorne, El Cajon, California. E. J. Newcomer of Yakima, Washington collected many specimens of *Euchloe* from that state for the author's examination. C. W. Sharsmith of San Jose State College kindly confirmed or corrected the author's determination of plant specimens. Margaret S. Bergseng of the University of California Herbarium determined two species of Cruciferae which were collected during the summer of 1965. My special thanks are extended to J. W. Tilden, H. T. Harvey, and C. W. Sharsmith, who read the thesis upon which these papers are based and helped to correct errors. Any errors which occur in these papers are the responsibility of the writer.

PART 2. CHRONOLOGICAL REVIEW OF THE LITERATURE AND BIBLIOGRAPHY

THE FIRST PORTION OF THIS PAPER will deal with the development of the concepts concerning the specific status of the *Euchloe* of the Nearctic Region. The second portion is a complete bibliographic listing of all of the literature which is cited in the papers of this series.

CHRONOLOGICAL REVIEW OF THE LITERATURE

In this review opinions of all authors which contain contributions to development of concepts concerning the status of Nearctic *Euchloe* are given. Personal interpretations are made by this writer for the sake of bringing clarity to past opinions which, in the view of the author, are often illogical or nebulous due to the presentation of insufficient information.

As an aid in evaluation of this study a brief synonymy of the names that have been proposed for Nearctic *Euchloe* is presented:

Euchloe (*Euchloe*)

1. *ausonides* (Lucas), 1852
 Var. *flavidalis* Comstock, 1924
 Var. *semiflava* Comstock, 1924
 ab. *boharti* Doudoroff, 1930
 (*coloradensis*) ab. *hemiflava* Field, 1936
 A. ausonides coloradensis (Hy. Edw.), 1881
 (*belia belioides*) race *montana* Verity, 1908
 B. ausonides mayi Chermock & Chermock, 1940
2. *olympia* (Edwards), 1871
 A. olympia rosa (Edwards), 1871
3. *creusa* Doubleday, 1847
 Var. *elsa* Beutenmüller, 1898
 (*belia*) var. *orientalides* Verity (Partim.), 1908
4. *hyantis* (Edwards), 1871
 (*belia*) var. *pseudoausonides* Verity, 1908
 A. hyantis lotta Beutenmüller, 1908 New Combination
 (*creusa*) ab. *pumilio* Strand, 1914
 (*belia*) var. *orientalides* Verity (partim.), 1908
 B. hyantis andrewsi Martin, 1936 New Combination

Doubleday & Hewitson (1847) named *Euchloe creusa* as the first entity of the genus for North America based on specimens collected in the Rocky Mountains of Canada by Lord Derby. [Westwood died before date of publication] No description was given, and the identity of the form was based only on a type specimen [not designated] and an inadequate plate figure.

Lucas (1852) described *Euchloe ausonides* on the basis of specimens collected in California by Lorquin. No figure was included, but lengthy descriptions of both sexes were given.

Boisduval (1852) mentioned the name *ausonides* in a paper on the butterflies of California. Boisduval was credited as the

author of the name in many citations due to a misunderstanding of publication dates. Dos Passos (1962) gave detailed information concerning the dates of publication of the papers in question on the basis of which Lucas is credited with the authorship of *ausonides*.

Edwards (1863) redescribed *ausonides* from California, Canada, and Colorado. It is interesting that this description could be applied to any of the Nearctic entities with the possible exception of *Euchloe olympia*.

Edwards (1871) described *Euchloe hyantis* from specimens collected at Mendocino City, Mendocino County, California by R. H. Stretch.

Strecker (1878) treated *ausonides* as a variety of *Euchloe ausonia*, a Palaearctic form.

Henry Edwards (1881) described *Euchloe ausonides coloradensis*. This name was proposed as a new species according to the taxonomic usage which was in practice at that time. The description included was just sufficiently detailed to establish the identity of the insect. The type was collected by T. L. Mead in June, 1871 while he was in Colorado with the Wheeler Geographical Expedition.

Beutenmüller (1898) wrote the only revision of the Nearctic *Euchloe* prior to the present study. In this revision the author revised his opinions from those expressed in his paper of 1897. He introduced two new names, *Euchloe lotta* described as a specific entity, and *Euchloe creusa elsa*, which has been subsequently treated as a synonym of *creusa*. The name *lotta* was proposed for the entity found in the Artemisian Biome and deserts of the southwestern United States. Previously, the name *creusa* had been applied to these populations, which Beutenmüller correctly realized were not conspecific with *creusa*. Although Beutenmüller's concept had an insight into relationships involved, he not only did not explain the reasons for his arrangement of the entities within the genus, but incorrectly considered the name *hyantis* to be a synonym of *creusa*.

Butler (1899b) published a paper in response to the work of Beutenmüller (1898) in which Butler stated that all Nearctic entities were forms of *ausonides*.

Beutenmüller (1899) stated, in a reply to the comments of Butler (1899b), "I concluded that it would be best to allow the species to remain distinct until more light could be obtained on the subject." He then proceeded to elaborate on his concept pertaining to the identities of *creusa* and *hyantis lotta*.

Browning (1901), in a faunal paper on the Rhopalocera of the Salt Lake City, Utah, region, figured a specimen of *hyantis lotta*. He correctly applied the name *lotta* to the specimen, but incorrectly assumed it to be a variety of *ausonides*, which can be seen immediately by referring to the above mentioned plate.

Franck (1905) stated that he believed the name *hyantis* to represent a subspecific entity of *ausonides* and that the name *coloradensis* was a synonym of *hyantis*. No basis was given for this idea.

The probable identity of *Euchloe* illustrated by Wright (1906) indicates that in only one or two cases is it possible that the collection data are correct.

Coolidge (1908) attempted to present an arrangement of Nearctic entities which would eliminate the wide range of differing treatments of the genus. He placed *lotta* and *hyantis* as subspecific names under *creusa* and placed *coloradensis* as a synonym of *ausonides*. This arrangement, in an only slightly modified form, was restated by Barnes and McDunnough (1916), and gradually assumed the position as the "correct" treatment of the Nearctic members of the genus. This concept was given no biological or morphological basis.

Verity (1908) attempted to enforce upon the new world members of the genus *Euchloe* a biological phenomenon which was well documented in the Palearctic Region, i.e., the occurrence of two morphologically distinct seasonal forms for each entity. Several unnecessary new names and some very unwieldy nomenclatorial combinations resulted. The types of *ausonides* and *creusa* were figured in this work.

Strand (1914) described an aberration *hyantis lotta* from Oregon by the name *pumilio*. He incorrectly used the name in combination with *creusa*.

Barnes and McDunnough (1916) gave a lengthy discussion of their opinions of the relationships of North American members of *Euchloe*. Although the authors reinforced the erroneous arrangement initiated by Coolidge (1908), they corrected the mistake by Verity concerning the presence of seasonal forms in the Nearctic Region by placing all of Verity's names in synonymy. They also correctly considered the name *elsa* to be a synonym of *creusa*, and raised *coloradensis* from synonymy as a subspecies of *ausonides*.

Barnes and McDunnough (1917) presented the arrangement of the Nearctic entities of the genus *Euchloe* which was to be followed for many years. The following citations repeated the

treatment of Barnes and McDunnough: Barnes and Benjamin (1926), Comstock (1927), and dos Passos (1964).

Comstock (1924) described two varietal color forms of female *ausonides*, which were collected from the populations which occur in the vicinity of San Francisco Bay, California. Comstock evidently did not know that one of these color forms, *semiflava*, is normal for the females of this species, since the hindwing of the female in other species does not show a contrast in pigmentation with the forewing. The variation in pigmentation of this group will be presented in greater detail in a later paper of this series.

Coolidge (1925) described the life history of *Euchloe hyantis lotta* on the basis of material collected in the western Mojave Desert of California. Coolidge repeated his mistake of an earlier paper (Coolidge, 1908) by associating the name *hyantis* with *Euchloe creusa*.

Comstock (1927) in "Butterflies of California" introduced two somewhat erroneous concepts which were perpetuated because of the popularity which this book attained. Although Comstock figured specimens of *ausonides coloradensis* from Colorado, he stated in the text that this subspecies "is occasionally taken in the high mountains of California". This statement led to the practice of referring to all specimens of *Euchloe* collected in the Sierra Nevada as "*Euchloe ausonides coloradensis*". Some small isolated populations of *ausonides* are to be found in the Sierra Nevada; however, most population of *Euchloe* in that range are *hyantis*. The latter situation and the fact that Comstock's treatment of *hyantis* was somewhat nebulous led to misunderstandings of *hyantis*.

Doudoroff (1930) gave to a melanic specimen of *Euchloe ausonides* the name *boharti*.

Klots (1930b) reported *E. creusa* from Teton County, Wyoming. Specimens from this collection have been examined by the author and proved to represent *hyantis lotta*.

Holland (1931) figured the type of *hyantis* and a specimen which may represent the type of *Euchloe hyantis lotta*. Holland treated the names *ausonides* and *coloradensis* conspecifically, and considered the names *creusa*, *lotta*, and *hyantis* to represent separate species. His statement of the distribution of the latter entities showed that he had no clear concept of their relationships.

Field (1936) described a male color form of *Euchloe ausonides* from Utah in which the "upper surface of the secondaries [was] suffused over with yellow". Not only did Field incorrectly attribute this specimen to the name *coloradensis*, but he may have been incorrect in assuming that it was a male.

Martin (1936) described a population of *Euchloe* from the San Bernardino Mountains of southern California. He gave to this race the name *andrewsi* in honor of the collector, R. H. Andrews. This population should be referred to as a subspecific category of *Euchloe hyantis* rather than of *Euchloe ausonides* as it has been treated.

Chermock and Chermock (1940) described *Euchloe ausonides mayi*, a distinctive population from the Riding Mountains of Manitoba.

Brooks (1942) erroneously considered *ausonides coloradensis* to occur in Manitoba.

Leighton (1946) reported *creusa* and "*Euchloe creusa hyantis*" as occurring in eastern Washington. The insects referred to by these two names were probably specimens of *Euchloe hyantis lotta*. Newcomer (1964) followed this procedure in reporting *creusa* from Yakima County, Washington.

Bauer (1953) applied the name *creusa* to *hyantis lotta* from Arizona.

Brown (1955) used the name *creusa* to represent specimens of *hyantis lotta* from western Colorado. Brown showed that he was aware of difference between *hyantis lotta* and *ausonides coloradensis* by his list of differentiating characteristics in the appearances of the two entities.

Powell (1958) and others have used the combination *ausonides andrewsi* to refer to specimens of *Euchloe* from the peninsular ranges of Baja California Norte. Populations of *Euchloe* from the peninsular ranges of southern California, and Baja California Norte, referable to *hyantis*, do not represent the names *andrewsi* or *lotta*.

Ehrlich and Ehrlich (1961) used the names *Euchloe ausonides*, *Euchloe olympia*, and *Euchloe creusa* to represent all of the entities of *Euchloe* found in the Nearctic Region. The authors state that *Euchloe creusa* "is only doubtfully distinct from *Euchloe ausonides*."

Garth and Tilden (1963) followed the usage of Comstock (1927) in reporting "*Euchloe creusa hyantis*" and *Euchloe ausonides coloradensis* from the central Sierra Nevada of California.

Storer and Usinger (1963) used the name "*Euchloe coloradensis*" in referring to a *Euchloe* found in the Sierra Nevada of California.

Dos Passos (1964) adds the dates of the original citations for all of the names involved, his arrangement is little changed from that of Barnes and McDunnough (1917)

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BUTTERFLY AGGREGATIONS

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PROBABLY A GOOD MANY COLLECTORS have, at one time or another, during their field trips seen butterflies accumulating, by the dozens and hundreds, in very small places. This is particularly true of the tropics.

Species belonging to certain families, particularly the Papilionids,, Pierids, Nymphalids, and Lycaenids are known to have this habitual tendency.

The habit to aggregate in large numbers has obviously developed from the feeding peculiarities of these insects. Feeding peculiarities, on the other hand, are greatly influenced by an irresistible attraction that certain odors impose on these butterflies. Very often it is just a natural dampness caused by rain or running water on roads, river banks, lakes, and sea shores, or other wet places that may attract these thirsty insects. Odors, sometimes very obnoxious to the human nose, caused by the decaying plants or animal bodies, human or animal excrement and urine, remnants of food, drinks, or of other materials, may attract butterflies in smaller or larger numbers.

In the following paragraphs I would like to report on a few cases drawn from my past experiences in the field.

PAPILIO GLAUCUS CANADENSIS IN ADIRONDACKS.

It was during a collecting trip in the Adirondacks, upper New York State, in June 1956 when this observation was made. The *Papilio glaucus canadensis* were out in large numbers. Only fresh males were flying and the very first females had just started to appear.

The shoulders of the dirt roads were actually swarming with these attractive yellow fliers, and particularly some of the dips on the road, where more moisture had accumulated, and also some damp roadside ditches seemed to attract the hungry insects.

On Schroon River Road, I drove on a gravel road running through a sparsely populated area and through a partially shady woods. At some distance from a small puddle in the middle of the road I stopped my car. My attention was attracted by a kind of activity on the damp gravel where some fifty males of *canadensis* were sitting side by side, all with wings closed, and enjoying the presence of moisture. I approached the spot as cautiously as possible, moving the last few feet on "all fours," fixed my camera at a distance of about two feet and took a few pictures. Not one specimen became disturbed. It was pleasantly quiet there without any movement in the air.

Next day I concentrated my attention on another dirt road leading from Indian Lake to Cedar River Flow. It was a nice warm day, June 17th, and the *canadensis* was again swarming along the sides of the road. I was looking for a larger aggregation of *canadensis* to get a few more pictures.

Smaller groups, consisting of about twenty to thirty specimens, were observed. Then, came what I was really looking for. On a dry gravel roadside, just about a foot or two from the very margin of the road, I noticed a large yellow spot. Low grass, sedges mostly, but no flowers, sparsely covered this roadside. It was on this yellow spot, measuring about one and a half feet in diameter, that I noticed about one hundred and twenty *canadensis* sitting, side by side, with wings closed. As I approached cautiously, a few flew away but I managed to take two pictures. Then I covered the spot with my eighteen inch collecting net. The entire aggregation flew up, and my large net was filled with frightened Papilionids. I started taking them out one by one, examining and counting the specimens, and afterwards giving them their freedom. Many escaped my counting but, nevertheless, I counted eighty-five in all. Without exception they were all fresh males, not a single female was among them. I examined the spot closely and concluded that either the presence of moisture or some curious odor was the reason for the aggregation.

PAPILIO GLAUCUS IN CATSKILLS.

One interesting observation comes from the Catskill Mountains in New York State. It occurred in July 1956. After collecting for half a day in the picturesque Big Indian Valley, I was approaching the end of the valley on a gravel road where it joins the highway. It was about three o'clock in the afternoon, and I was getting hungry.

Stopping my car under a shady birch, I was ready to open my lunch box when I saw a movement. It was in a dry pasture, and I had to climb a stone fence to get closer. What attracted me was fresh cow dung on which a large variety of butterflies were feeding. I covered the fresh brown mass trying not to smear my net. After I sorted the insects from my net there were about fifty *Papilio g. glaucus*, four *Limenitis arthemis*, and two *Limenitis a. astyanax*. This is a good example that the animal excrements sometimes attract a large number of certain butterflies. This time they were Papilionids and Nymphalids.

PAPILIONIDS IN THE SMOKIES.

Speaking of the Papilionids, another experience comes to my mind. Collecting in the Smoky Mountains of Tennessee on May 15th, 1960, there were many *philenor*, *troilus*, and *glaucus* flying in the afternoon along the gravel road in one of the canyons. The *philenor* outnumbered the other two, and there were very few *glaucus*. There seemed to be more specimens around the picnic places and on the sections of the road where water was dripping from the canyon walls. I had to descend to the river in order to wash my hands, and while walking down my attention was attracted to a small hole between the rocks. In the hole, which was no larger than eight inches in diameter, there were a dozen or more butterflies sitting. Most of them were quietly sucking, however, a few were moving around restlessly. I covered the hole with my net and caught all of them and examined them. There were: eight *glaucus*, three *troilus*, six *philenor*, three *Erynnis horatius*, and three *Epargyreus c. clarus* in this social company. There was very little moisture in the hole. I found four *glaucus* wings and what looked like the remnants of their decaying bodies. It was my impression that someone had stepped on a few *glaucus*, which were sucking on moisture, and that this was responsible for the hole. The possibility also exists that a reptile, like a lizard, partly consumed the *glaucus*.

I stepped down to the stream and continued my observation of the place for any further development. After awhile, a male *glaucus* was flying above the middle of the stream. As it approached me it veered sharply in the direction of the hole, where it landed with the velocity of a bullet. Another male *glaucus* repeated the same maneuver a few minutes later. No doubt, all

the above insects were attracted to the place by the odor of the decaying bodies of the dead butterflies, an odor not perceptible to the human nose but very much perceptible to the fine olfactory organs of these butterflies.

This last incident reminds me of another day of collecting in the Adirondack Mountains of New York. After catching my first *glaucus canadensis* in the morning, I squeezed its body and discarded the specimen on the road. I remained at the same place to catch other *glaucus* that were flying by. I collected about twenty males in one hour, either sitting on or flying around the dead specimen. It was amazing to see even other specimens, which were flying by on the opposite side of the road, suddenly crossing the road to land on or near the dead specimen. In this case again, there was no doubt that it was not the yellow coloration of the dead specimen that attracted the males so persistently but the odor of the dead body. I repeated this procedure in the afternoon but it seemed to work only in the forenoon and only with freshly squeezed specimens. When a dozen males, which were squeezed in the morning and dried during the day, were placed in the same area early next day these bodies did not attract any butterflies.

HAIRSTREAKS.

These are another group of butterflies which occasionally tend to aggregate in one place particularly preferable to them from the standpoint of feeding. I have had several cases where I encountered large numbers of one or more species of *Strymon* sitting on one large flowering plant. These are my observations.

On a trip through the Oklahoma Panhandle to New Mexico several stops were made along the highway in Dewey County, south of Seiling, Oklahoma. In those places the large yellow spots on the roadsides indicated the presence of one of the most desirable plants, Butterfly Milkweed (*Asclepias tuberosa*), to hairstreaks and to many other diurnals. It was in June 1952, and the plant was in full bloom.

I approached one yellow cushion, about two feet in diameter, and I noticed that it was so densely covered with *Strymon* that there was hardly a place for additional ones. An estimation was made that there were more than two hundred specimens on that plant. From one corner of the plant I was able to gather the following: Ten males of *Strymon titus mopsus*, twenty-nine males and two females of *Strymon ontario autolytus*, and twelve

specimens of *Strymon f. falacer*, all together, fifty-three hairstreaks. A more careful study of other similar plants in that area disclosed that *titus mopsus* made up about twenty percent of the entire number of specimens sitting on one plant. The rest being about equally divided between the other two *Strymon*, namely the *falacer* and *ontario autolytus*. Besides the hairstreaks there were a few *Melitaea i. ismeria* and a few Hesperids. It also should be pointed out that the *titus mopsus* specimens were all fresh, *ontario autolytus* very fresh to fresh, and those of *falacer* fresh to worn.

Four days later, while returning the same way, a stop was made at the described place of the Butterfly Milkweed and the entire picture repeated itself. Same species of hairstreaks were collected on the plant, except that they were not as fresh this time. Besides the *Strymon*, there were a few *Nathalis iole* and *Vanessa cardui*.

In similar surroundings I had a commensurate experience in April 1953 on a highway four miles west of Mineral Wells, Palo Pinto County, Texas. The flowering Butterfly Milkweed plants on the roadside were covered with hairstreaks. I chose one of the more spectacular plants and after covering it with my net I had it full of *Strymon*. Some four or five dozen were collected. These made a small compromised part of all that were feeding on the plant. Unfortunately, I was not immediately cognizant of what species these *Strymon* represented. After it was checked at home, it turned out to be *ontario autolytus*, a species having its main distribution in Oklahoma and Texas, and in parts of some adjacent states. These are quite desirable to collectors. There were only single specimens observed on plants other than Butterfly Milkweed in that area. Only a few were collected while flying in a nearby oak thicket. The next year I returned to the same place to get more of the species. Unfortunately, the entire area, including that plant life, was changed because of the construction of a new road.

The third case of a mass occurrence of *Strymon* was observed in a different biotype involving another kind of plant. This time it was in June 1958 in Boiling Springs State Park, Woodward County, Oklahoma. The species involved was *Strymon a. alcestis*, and the plant that attracted this species was the Hemp Dogbane (*Apocynum cannabinum*). The plant was in full bloom at that time. The weather was very hot and humid: 105 degrees; with about 80% relative humidity. At this particular time of the year the above mentioned temperature and humidity are not unusual

for this part of the country. Following a female *Asterocampa antonia* in a small forest glade not far from the Park spring I discovered a dense growth of Hemp Dogbane. On almost every plant several *Strymon* were feeding or flying from blossom to blossom. I collected several *alcestis* males, partly worn, and females, nearly fresh. Besides *alcestis* there were only a few other butterflies present. Namely, *Strymon cecrops* and *Atalopedes campestris*.

The most recent observation involving one of our most common Lycaenids, *Celastrina a. pseudargiolus*, was made in March 1961 in the Great Smoky Mountains National Park. In two different canyons, one on the Tennessee and the other on the North Carolina side of the Park, this species, which had been very plentiful that year in the Smokies, was seen aggregating in groups of fifty to three hundred specimens. These groups were found accumulating in spots on the gravel roads.

What exactly attracted the "blues" in such numbers can only be guessed at. Possibly remnants of food or drinks left by picnickers, or it could have been gasoline from a leaky car. Anyway, the "blues" were so absorbed in their activities that one could almost step on them without disturbing them. In one place a few other species were associating with the "blues," but only as single specimens. Namely, *Papilio g. glaucus*, *Graphium marcellus*, and *Erynnis juvenalis*.

SKIPPER.

Hesperiids seldom tend to accumulate in one place in great numbers, but there are exceptions. I have seen *Erynnis*, sucking by the dozens, on damp spots on the roads, particularly in the morning and forenoon. But what I observed in April 1960 at Fall Creek Falls State Park, Tennessee, was something unusual. The fresh males of *juvenalis* were plentiful on the Park roads, particularly on road bifurcations and in parking areas.

When I came to a camping area reserved for organized groups, where a number of cabins and a larger building with a kitchen were occupied by some biology students, I observed the following: around the mess hall, where some food was being cooked, swarms of *Erynnis juvenalis*, estimated at about two hundred, were flying around the damp foundation of the building. They were on both the shaded and the sunny sides of the building. Whether or not it was the foundation dampness or some kitchen odor which attracted them I do not know. I lean toward the interpretation that the dampness and the peculiar odor of the

foundation was the main attraction. A dozen specimens could be netted at one sweep. All of them were fresh males and in a large majority belonged to *juvenalis*. Only two fresh *Erynnis persius* males and a few *Erynnis brizo* males were among them.

Another time, the following observation was made on a gravel road in the Smokies of Tennessee, May 1960. After leaving my car on a stream bank, I saw accumulations of *Erynnis icelus* in spots no larger than a foot wide. I tried to count the specimens aggregated in one of these places. There were twenty to thirty *icelus* sitting close together in one spot, no wider than three or four inches, and seemingly feeding on something. A closer examination did not reveal anything in particular which could have attracted the skippers. There was no dampness present. The gravel was entirely dry. But, people had been eating in this area, and possibly some spilled juice, Coca-Cola, beer, or remnant of food dropped in this place were attracting the insects.

LIBYTHEANA IN RIO GRANDE.

Libytheana bachmanii is a species that one usually catches just a few specimens at a time in places where the Hackberry, its food plant, grows. Seldom does one see large numbers of this species in one place.

In October 1951 while on a highway three miles east of Laredo, Texas, I tried to catch a few fresh *Kricogonia lyside* that were flying around in large numbers and I stepped into swarms of *bachmanii*. All the grass along the roadside and in the shallow ditch, mostly on the south side of the road, was covered with fresh specimens. There was a very light southerly breeze present.

My first impression was that the butterflies were migrating. But the specimens seemed to be very fresh, as if they had just emerged, and not flying around or going in any one direction. They seemed to be disturbed only by my footsteps in the grass. It seemed that in some spots there were more of them congregated, and stepping into those spots, I caused thirty to forty specimens to fly around for a short while and then settle down again in the grass. At times, when the breeze got stronger, swarms of *bachmanii* flew across the road in a northerly direction. Perhaps it was a migration, and the butterflies were resting there from the previous day's flight. This mass occurrence of *Libytheana* continued for miles and miles with changing density and there were millions of specimens along the highway.

I moved farther east as the daytime advanced. The southerly breeze increased, and swarms crossing the road contained a large number of *Kricogonia* and single specimens of fresh *Phoebis agarithe maxima*. Mass occurrence of *bachmanii* continued throughout that day, while I traveled a distance of about ninety miles toward Rio Grande City. Of course, they were a nuisance to my collecting! The next day, as I continued my way toward McAllen, there were still a large number of specimens flying around but not the swarms of the previous day.

Was this a migration from Mexico or just an unusual mass occurrence of this species that year along the Rio Grande? I do not know.

NYMPHALIDS IN COLORADO.

I have seen large numbers of Nymphalids, *Limenitis archippus watsoni*, *L. arthemis astyanax*, *Anaea andria*, *Asterocampa celtis*, *A. clyton*, *A. texana*, and *A. antonia* in Oklahoma and Texas gathering on fallen rotten fruit, particularly decaying peaches and pears. The fig orchards in Louisiana, for instance, are a good place to collect Nymphalids like *Polygonia* and *Asterocampa*.

The following observation was made on different butterfly species and on different bait during a collecting trip in July 1949 in Walnut Gulch, in Gunnison County, Colorado at an elevation of about 9000 feet.

Pursuing the interesting *Euphydryas maria alena* in that narrow gulch, I noticed a small aggregation of some twenty butterflies, *Melitaeini* and *Lycaenini*, sucking on a small amount of black excrement of an undetermined origin. When I returned five days later, after it had rained several times, my attention was again drawn to the above mentioned spot. I was fortunate enough to get most of the butterflies I found sitting on the same bait. The ones I collected consisted of: *Melitaea palla calydon*, *Phyciodes camillus*, *P. tharos pascoensis*, and *Lycaena amyntula*, with single specimens of *Thorybes nevada* and *Erynnis persius fredericki* among them.

The bait was kept under observation for thirty minutes, and the same species kept coming and alighting on the excrement. Other species were flying at the same time along the dirt road and around the same spot but none of them seemed to be interested in the bait. These species were *Papilio rutulus*, *P. bairdi brucei*, *Colias alexandra*, *C. scudderi*, *Pieris napi macdunnoughi*, and *Oeneis uhleri reinthali*.

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IN THIS ISSUE

Forelegs of Butterflies I. Introduction: Chemoreception Richard M. Fox	1
A New Species of <i>Epinotia</i> Hubner from British Columbia (Olethreutidae) T. N. Freeman	13
Studies in the Life Histories of North American Lepidoptera California <i>Annaphila</i> II. J. A. Comstock and C. Henne	15
New Skipper Records for Mexico H. A. Freeman	27
A Moth Sheet Noel McFarland	29
Cover Photo: <i>Daritis ? howardi</i> Hy. Edw. larvae Noel McFarland	36
Rediscovery of <i>Annaphila casta</i> Hy. Edw. in California (Noctuidae) John S. Buckett	37
Studies on the Nearctic <i>Euchloe</i> . Parts I, II Paul A. Opler	39
Butterfly Aggregations Walfried J. Reinthal	51

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THE JOURNAL
OF RESEARCH
ON THE LEPIDOPTERA



MORPHOLOGY OF THE IMMATURE STAGES OF *EVERES COMYNTAS* GODART (LYCAENIDAE)

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KNOWLEDGE OF THE EXTERNAL MORPHOLOGY of the immature stages of butterflies is quite incomplete. Most of the past work has dealt with moths, and on groups which many researchers consider the more "generalized" immature Lepidoptera. The more "specialized" groups, including the Lycaenidae, have been neglected. It is hoped that this detailed study of one species will provide a morphological platform on which to launch more intensive comparative studies within the family. To that end we have arranged the description of the larval morphology by individual structures rather than the more conventional treatment of describing each instar. This makes more emphatic the ontogenic changes in addition to any individual variations. The latter must be recognized before the former become meaningful.

Everes comyntas Godart is common throughout the Nearctic region and its range extends southward as far as Costa Rica. Eggs and larvae are found on white clover (*Trifolium repans* L.), red clover (*T. pratensis* L.) and lespedeza (*Lepedeza stipulaceae* Maxim.). Pupae have also been found on lespedeza and curly dock (*Rumex crispus* L.). Details of the population dynamics of this species will be published elsewhere.

PREVIOUS DESCRIPTIONS OF THE IMMATURE STAGES

Edwards (1876) gives an account of the early stages of *Everes comyntas* and gives measurements of the egg, larval stages and pupa. No illustrations were included. Scudder (1889) describes and gives three illustrations of the egg, including two views of the micropyle (*loc. cit.*, Vol. 3, Pl. 68, figs. 5 and 12) and an oblique view of the entire egg (*loc. cit.*, Vol. 3, Pl. 65, fig. 20). The latter appears to us to have too few reticulations in the surface. The same author has illustrated a dorsal view of the first instar larva, several head capsules, and pupae, all of which are accurate but, partly due to small size, lack specific details. Dethier (1941) pictures the larval antenna of *comyntas* in his

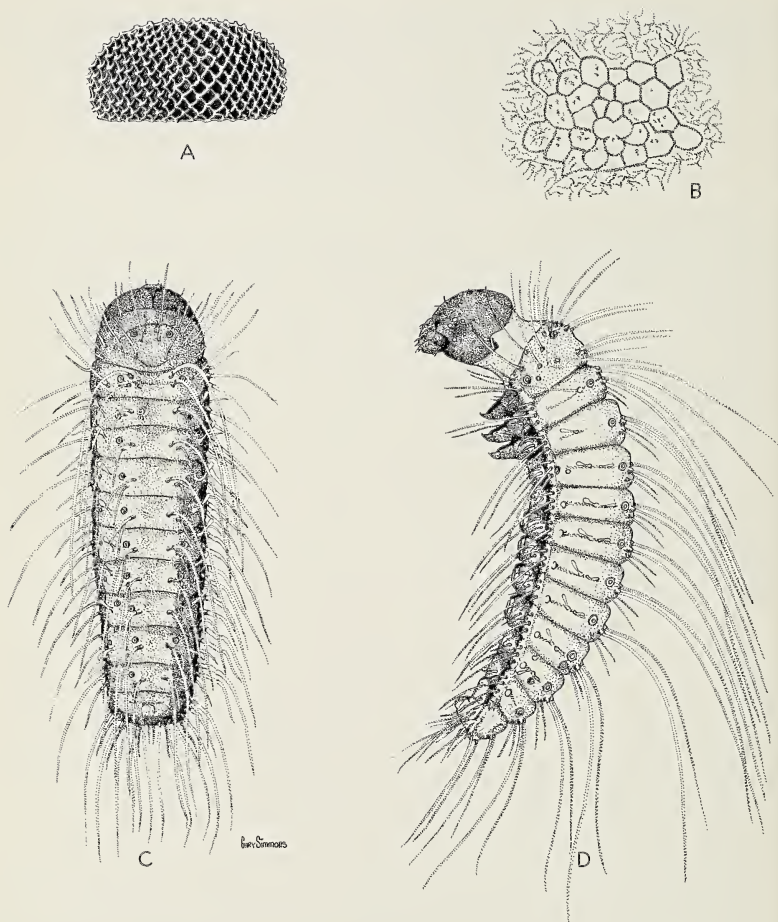


Fig. 1. Immature Stages of *Evers comyntas* Godart.

A—B. Egg; A. Lateral view, B. Dorsal view of micropylar area. C—D. First instar larva; C. Dorsal view, D. Lateral view.

comprehensive paper on the antennae of Lepidoptera. The immature stages are superficially described or illustrated in several other more general works, but these are overly simplified and are usually not diagnostic either of the species, or in some cases, the family.

THE EGG

Figure 1B is a lateral view of the egg which shows its typical lycaenid form. It is of turban shape, flat on the bottom and less noticeably truncate on top. The sides and top are covered with reticulations which are slightly elevated from the surface. Rounded prominences are found at the intersections of this network of ridges, giving the egg the appearance of an echinoid test. The diameter is 0.6 mm; the height, 0.3 mm.

The micropylar area (Fig. 1B) is only slightly depressed into the central vertical axis of the upper surface. Its central cavity consists of either three or four petal-shaped cells, open at their bases. These central cells are surrounded by other cells whose walls are of similar structure except that each cell has a complete wall. They vary from semi-round to hexagonal in shape. From one to three of these cells may occur between the petal-cells and the transition zone (see below). The walls of all cells in the micropylar area are uniform in thickness and appear to have a slight greenish tint under high magnification. Various unknown inclusions showing this same tint occur in most of the peripheral cells of the area. This region of the egg is of the same general type as other Nearctic *Plebejini* but is diagnostic of this species.

There is a small transition zone between the area of the micropyle and the elevated reticulations which characterize the dorso-lateral margins and sides of the egg. Although the lateral limits of this zone are often difficult to judge, the region is dissimilar to the other areas in that there is no regularity or uniformity to the walls of the opaque cells involved.

Radiating out from the transition zone is a network of raised, solid ridges arranged in tolerably regular oblique rows running across the top and down the sides of the egg. These are connected by another series of slender ridges which also run in an oblique direction, but at right angles to the first ridges.

As indicated above, there is a slight prominence or knobby elevation at the intersection of each ridge. The knobs are largest and most obvious on the sides and obsolescent near the transition zone and on the ventral surface. The ridges appear to be continuous with the walls of the cells in the transition zone, but they are marked by their elevation, prominence, knobbed intersections and regularity. The surface of the egg opposite the micropyle contains hexagonal cells, defined by their walls, which are uniform in thickness and, except for their regular shape, resemble the cells in the transition zone on the dorsal

surface. The areas between the walls are transparent in hatched eggs, though the entire area may be obscured by the substrate of maternal origin used to attach the egg to a surface.

In the living egg the thickened ridges appear white in color while the depressed areas between them are light green, reflecting the embryonic contents. A slight darkening of the punctuations occurs before hatching, or if the egg is parasitized. The general appearance of the egg, size, reticulations and micropylar area are distinguishing features which help separate this species from allied forms.

THE LARVA

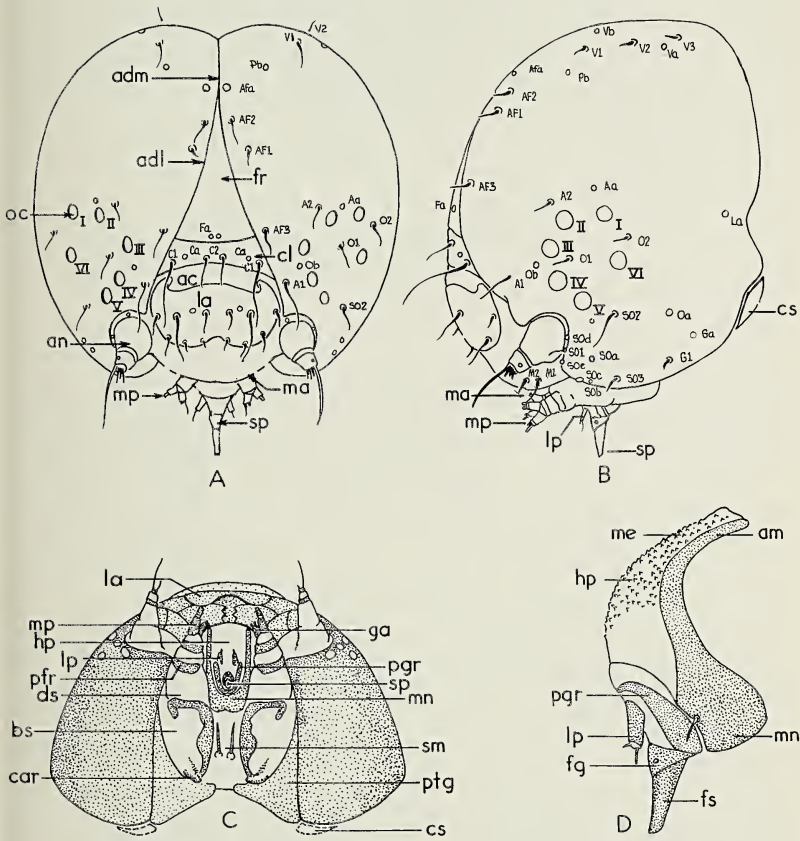
CRANIUM: The terminology of the sclerites and sutures of the cranium, especially as concerns the lepidopterous larva, has undergone much revision in the past two decades. Short (1951) reviews the various studies concerned with determining the nature of the sclerites and sutures of the cranium. One can only conclude from this review that no set of terms has as yet been worked out which would be satisfactory to all entomologists. The system of Hinton (1947) has been used herein with slight modifications when referring to specific sclerites or sutures.

The cranium of *E. comyntas* lacks conspicuous lateral cleavage lines (frontal sutures of Hinton or adfrontal sutures of many authors), see Fig. 2A. Other lycaenids including *Plebejus icarioides* (Bdv.) and *Plebejus melissa* (Edw.) also lack these frontal sutures. Most moth larvae have the sutures, although as Ripley (1923) points out, they may not appear except in the mature larvae. These lines are not mentioned by Clark and Dickson (1956) in any of their detailed studies on numerous species of South African lycaenids.

Measuring the head capsule width is a reliable method for determining the four larval stages of this species. There is no overlap of head capsule width between instars. The ranges of head capsule width are as follows (measured between widest points):

First Instar	.186—.207 mm.
Second Instar	.285—.313 mm.
Third Instar	.492—.519 mm.
Fourth Instar	.855—.923 mm.

In addition, a nearly constant 1 to 1 ratio was obtained in all instars by dividing the width of the fronto-clypeal apotome (taken as the distance between seta C1 on the right side and C1 on the left) by its length (taken as the distance between the anteclypeus (ac) and apex of the triangle formed by the lateral adfrontal sutures (adl) (See Fig. 2A).



Crumb (1929) found many positive differences in the arrangement of the head setae and punctures in different species of Noctuidae, with a strong tendency toward generic homogeneity. The same author cautions, however, that the degree of individual variation necessitates the examination of a series of specimens before positive conclusions are drawn. In the discussion below of the setae and punctures, the "normal" position or arrangement is given only after numerous larvae of each instar were studied.

Chaetotaxy of the cranium: Even more than the cranium, larval chaetotaxy has afforded much discussion in the literature, often involved with attempts either to homologize or to compare the systems used in specific cases by various authors. Thus Peterson (1951) gives a table comparing names used by Forbes and Heinrich; Mutuura (1956) tabulates and compares the systems of Fracker, Gerasimov and Hinton with his own; and Hasenfuss (1960) compares the chaetotaxy systems of Gerasimov, Hinton and Bollmann. McKay (1963) discusses some problems and briefly compares certain setae of Mutuura and Hinton, but uses the system of the latter. The reader is referred to these authors for specific details on nomenclature and homology. We have used the terminology of Hinton (1946). For ease in following the discussion of the setae below, the reader is asked to refer to Figs. 2A, 2B and 3H. Setae and punctures of the left side only are discussed unless otherwise indicated.

Frontal (A) and Clypeal (C) Setae and Punctures: In the first and second instar the longest seta, C1, is found in the lateral angles of the isosceles triangle formed by the lateral adfrontal sutures. Just medial to C1 is a puncture, here called Ca, not mentioned by Hinton. About two thirds of the way to the midline from C1 is another seta, C2, slightly shorter than C1. Above C2 on the frons but nearer the midline is a puncture Fa. No other setae or punctures are found within the triangle on the first or second instars. With each succeeding instar Ca is proportionately nearer C1 than C2.

Another, smaller, clypeal seta is found on the third instar just medial to Ca. Anywhere from one to four additional setae may be found above the frontal puncture and within the triangle.

Three clypeal setae not found on the first instar are found on the fourth instar between C2 and Ca. Their position is variable within this area and some of them may be absent. As few as six and as many as eleven setae may be present above the frontal punctures and within the triangle on the fourth instar.

Adfrontal Group (AF): In the first instar lateral to and paral-

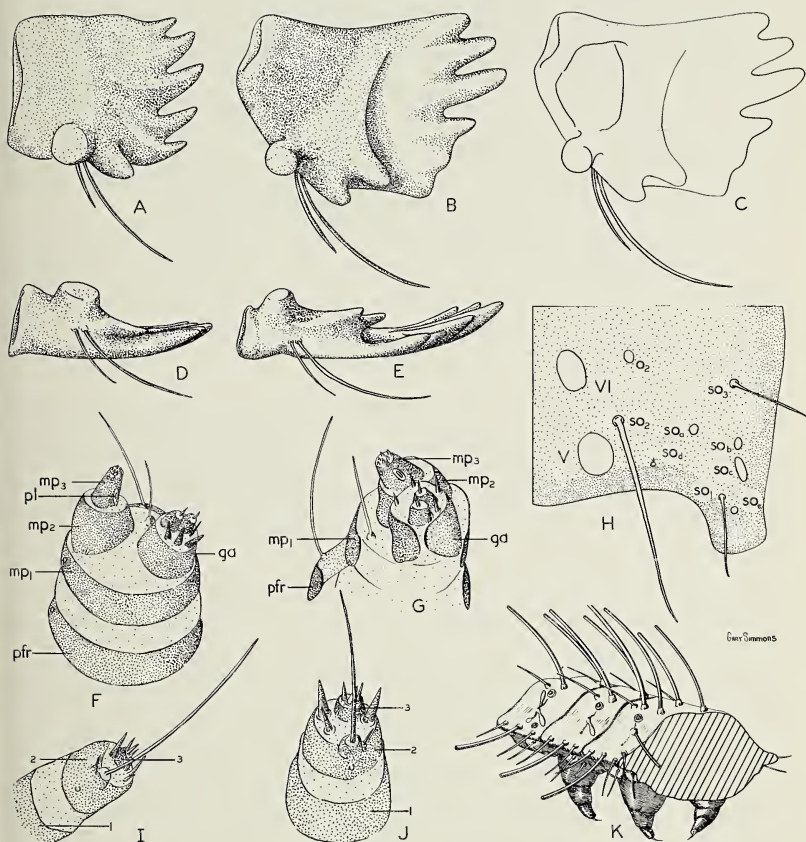


Fig. 3. A—E. Right mandible; A. First instar, oral aspect. B. Fourth instar, oral aspect. C. same, line drawing of optical section. D. First instar, edge, posterior aspect. E. Fourth instar, edge, posterior aspect. F—G. Maxilla; F. Left maxilla frontal-dorsal view. G. Right maxilla frontal-dorsal view. H. Chaetotaxy of the left subocellar area, head capsule, first instar larva. I—J. Antenna, frontal-lateral view. I. Fourth instar. J. Second instar. K. Schematic section through meso-thorax of first instar larva showing lateral ridge and position of major setae on several adjacent segments.

ling the lateral adfrontal suture are three setae and a puncture. These are called respectively from the lower-most to the upper-most; AF3, AF1, AF2, and AFa. The setae are roughly equal in length with AF2 sometimes shorter. AF3 is usually found on a horizontal line with the frontal punctures Fa. AF2 and AFa are variable in relation to one another and have been found with their positions reversed on later instars. No change in

arrangement and no additional setae or punctures are found within the area of this group on any of the succeeding instars.

Anterior Group (A): Two setae and a puncture make up this group on the first instar with the longer seta (A1) just above the antenna. A2 is caudal to A1 and is about one-fifth to one-fourth its size and is associated with ocellus II. The puncture Aa is caudal and somewhat lateral to A2. It is more closely associated with ocellus II in the first instar than in later instars.

Puncture Aa is about equidistant from ocellus I and II in the second and third instars, but on the fourth instar it is usually closer to ocellus I. An additional seta is found within this group in some third instars. In individuals of the fourth instar as many as three additional setae may be found.

Ocellar Group (O): The ocellar setae are about equal in size. Seta O1 is usually equidistant from ocellus II and III. Seta O2 is caudal to O1 and ocellus I, but usually nearer to ocellus VI. Puncture Oa is caudal to ocellus V and below ocellus VI, but with each succeeding instar takes a more caudal position with respect to the latter.

Rarely there is a third seta just caudal to ocelli IV and V on the third instar. This additional seta is constantly present on fourth instars.

Subocellar Group (SO): On the first instar SO2 is the longest seta of this group and is located just behind ocellus V. It is slightly longer than seta A1. Seta SO1 is found just lateral to the antenna between two punctures, SOd and SOe, and is a third to half the size of SO2. Seta SO3 is caudal to SO2 and is about equal to it in size. There are five punctures in this group, but only SOa is named by Hinton. This is located below SO2. The others have been mentioned in relation to SO1; the other two, SOb and SOc, which are closely associated are located below SOa. Puncture SOc is peculiar in shape and is much longer than wide in comparison with other punctures. It is very constant in position and may have taxonomic significance. Apparently most larvae in the Lepidoptera do not possess this puncture, at least it is lacking in most figures and illustrations.

The second instar has the same arrangement as the first. Additional subocellar setae variable in number and position can be seen on the third and fourth instars.

Lateral (L) and Genal (G) Setae and Punctures: On the first instar puncture La is considerably behind ocellus I. Seta G1 is a very minute seta located on the gena. Behind G1 and above it

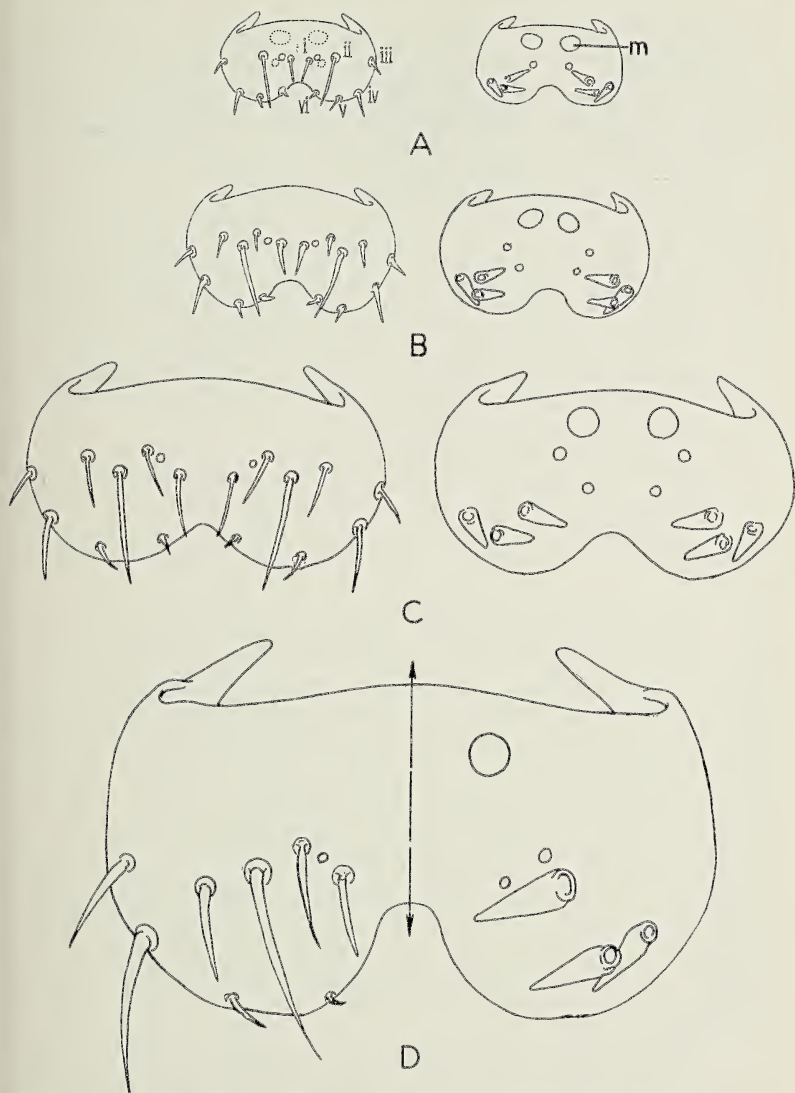


Fig. 4. A—D. Labra of larvae, showing setal pattern, facial aspect on left and oral aspect (epipharynx) on right of page. A. First instar. B. Second instar. C. Third instar. D. Fourth instar right half of labrum only.

is the puncture Ga. The distance between G1 and Ga is quite variable, but positional relationships are constant.

No additional lateral or genal setae and/or punctures are found on the later stages. The distance between G1 and Ga on the third and fourth instars is much more constant, however.

Posterior Group (P): Hinton's posterior group is made up of two setae and two punctures, but only one puncture of this group is found on *E. comyntas*. This particular puncture is called Pb and is so closely associated with the setae and punctures of the vertex that it would seem to belong to this group. Puncture Pb is found on all instars in the same position.

Setae and Punctures of the Vertex (V): Behind Pb and extending caudally is a group of three setae and a puncture; V1, V2, Va, and V3 in order. The setae are all minute and about the same size as G1. They are constant in position on all instars. Medial to V1 and V2 is a puncture for which Hinton shows no homology unless it represents a puncture formerly belonging to the adfrontal or posterior group, which has migrated in a caudal direction. It is here considered as Vb.

Appendages of the Head. The Labrum, Epipharynx: the labrum, Fig. 4A to 4D, does not differ greatly from that of any other lepidopterous larva. It is notched, but this is not unique and the depth of the notch is subject to considerable individual variation.

The typical first instar labrum bears six pairs of setae on its facial surface (see Fig. 4A) and three pairs of broader more bladelike setae on the oral surface, more properly termed the epipharynx. (Unless otherwise indicated the setae and punctures in the following discussions are those of the left side only.) The setae are labeled following the system used by Forbes (1911). Seta *i* is located on the labrum near the midline, about halfway between the distal margin and the anteclypeus. A puncture is found lateral to, and somewhat behind, seta *i*. Setae *ii* is the longest seta of the group and is located lateral to seta *i*. Of the four marginal setae, seta *iii* is the most posterior of the series and is on the lateral margin; seta *iv* is the longest of this group and setae *v* and *vi* are both subequal to *iii* and are the smallest in the series.

The arrangement of the setae and punctures on the labrum of the second, third, and fourth instars is the same except the possible inclusion of one or two additional setae in the fourth instar.

The first instar larvae has one, and the other instars two, punctures on the epipharynx. The blade-like setae do not vary in structure and change but slightly in position between instars. The apices of these peculiar structures are directed toward the mid-line and when seen from below, appear to project slightly into the pre-oral cavity. Each appears to have a circular clear

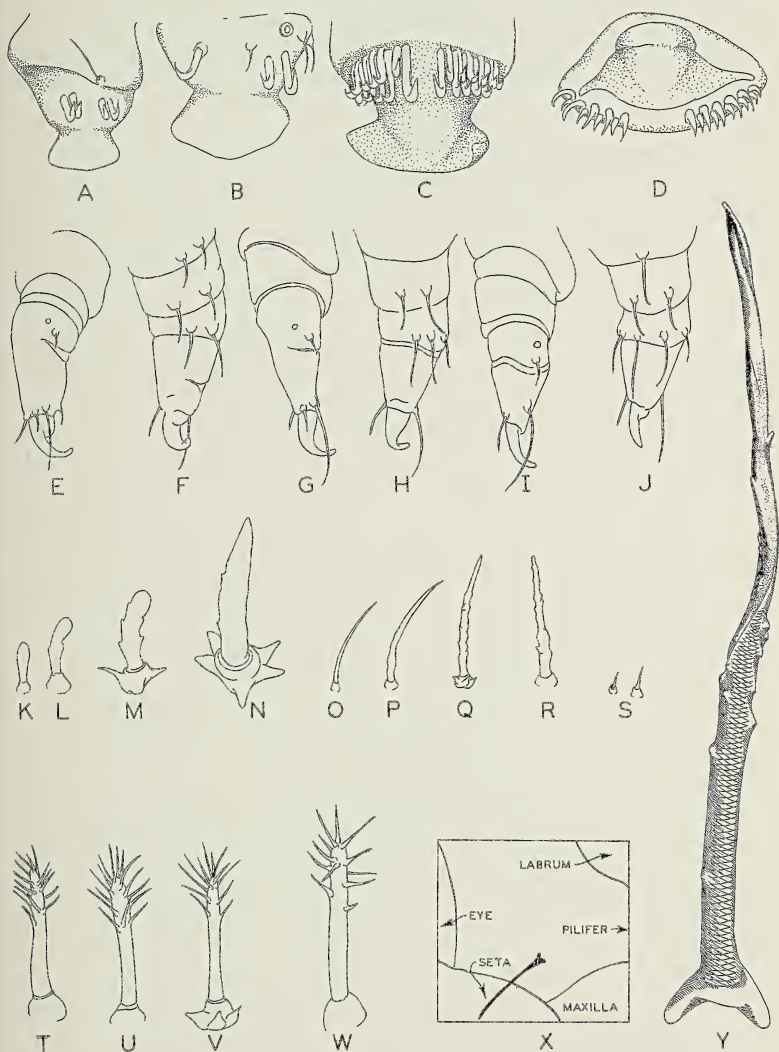


Fig. 5. A—D. Distal prolegs of larvae showing arrangement of crochets; A. Medial view of proleg, first instar. B. Medial view, anal proleg, first instar. C. Medial view of proleg, fourth instar larva with fleshy spatulate lobe below crochets. D. Ventral view of same. E—J. First instar Thoracic legs; E, G, I, lateral views of left pro-, meso- and methathoracic legs. F, H, J, medial views of right pro-, meso- and methathoracic legs. K—N. Type C setae from first (K), second (L), third (M), and fourth (N) instar. O—R. Longest seta on dorsum of fourth abdominal segment from first (O), second (P), third (Q), and fourth (R) instar larvae. S—microsetae from first instar larvae. T—W. Spiculate setae from second (T), third (U), and fourth (V) instar larvae and from the pupa (W). Y—example of major seta from head of pupa from location shown in X.

area near, but not at the base, which perhaps represents the internal out-pouching of the integumentary wall. The function of these setae is unknown, but they would certainly appear to be useful in holding or helping direct the food between the mandibles.

A pair of muscle scars (marked "m" in Fig. 4A) are prominent features of the proximo-mesial surface of the epipharynx.

The Antennae: The antennae (Figs. 2A and 2B, 3I and 3J) do not differ radically from those of any other lepidopterous larva. They are located on the head, ventral and medial to the ocelli. Ferris (1943) pointed out that the antennae of lepidopterous larvae have lost their point of articulation with the antennal segment and arise from a basimandibular membrane, no longer within the boundaries of the sclerotized cranium. In *E. comyntas* larvae, the bases of the mandibles and antennae are in close proximity and the latter often remained attached to the former when they were teased from the cranium. The membranous area at the base of the antennae is called the antacoria. From the antacoria arise the three main segments which comprise each antenna. On the second segment are a long and a short seta, two conical projections, and one small seta-like projection. A puncture is located on this segment midway between the long seta and the proximal margin of the segment. On the third segment there is one conical projection and two smaller seta-like projections. A very minute projection, not easily seen, is also located on the third segment.

Dethier (1941) pictures a larval antenna of *E. comyntas*. The only differences noted between his drawing and our specimens are that the small seta on the second segment is much larger, and the seta-like projections are much smaller than the corresponding structures on the specimens examined during this study.

Measurements were taken to determine the antennal lengths of the various instars. Exclusive of the long seta and including only the three segments, the lengths in microns were: first instar, 16.6; second instar 32.2; third instar, 51.6; and fourth instar, 100. The lengths in microns for the long seta were 58.2, 74.6, 100, and 161 microns respectively.

There is some variation in antennal length between individuals of the same instar, and also, a degree of variation in ratios of component segments of the antennae between instars. Segment 2 became proportionately longer than segment 1 and 3 with each succeeding instar.

The Mandibles: The mandibles, Fig. 3A to 3E, have anterior and posterior articulations with the head capsule. The former occupies most of the flattened region on the side of the mandible opposite the incisor edge. The posterior articulation is by means of a rounded, knob-like condyle which is a convenient landmark on the posterior mesial edge of the mandible. The first instar mandible (Fig. 3A) has sixth teeth, the most posterior of which is somewhat elevated and associated with the condyle. From the latter prominence a ridge, or retinaculum, runs across the mandible to the anterior surface. Sclerotized crests run from the teeth to the retinaculum and, particularly with the second and fourth tooth from the posterior end, give the impression of distal linear folds. Two setae, one long and one short, are present on the posterior lateral margin. Later instars (Fig. 3B) have seven teeth, the distal incisor points varying somewhat in shape. Three of the middle points are almost finger-like, while the more anterior and posterior teeth in the series may be reduced and blunted.

It would appear that the retinaculum becomes gradually elevated in progressive instars, particularly along the posterior parts of the mandible. Teeth are either incorporated in this retinaculum (the most posterior tooth in the first instar mandible appears closely associated with the prominence) or develop there, so that the retinaculum of the fourth instar larva is characterized by two prominent teeth. The appearance and ontogeny of these structures is best seen in Figure 3D (first instar) and 3E (fourth instar). The two molar teeth are suggestive of the basal molar parts observed in mandibles of some Coleoptera. They are at a different level than the dentation of the distal margins.

Of some interest is the fact that Crumb (1929) noted that decided peculiarities in the mandible were "invariably associated" with a wide departure in position and arrangement of setae and punctures on the head. We were not able to notice any such correlated anomalies.

A little degree of orientation may help the reader in locating the next four head appendages. If the head capsule of a fourth instar larva is viewed from the ventral surface (Fig. 2C) a pair of maxillae are conspicuous on either side of a centrally located labium. Closer inspection of the maxillae shows four distal sclerotized rings, the three most distal of which are the maxillary palps. Actually the terminal portions make up an outer palpus. There is a less conspicuous inner lobe of the palpus (the galea) on the dorso-mesial surface. Details of these structures are given be-

low. The fourth sclerotized band from the tip of the maxillae is the palpifer. The latter attaches to the stipes, the distal parts (dististipes) of which are membranous. The proximal area of the stipes is outlined on its distal and mesial extremities by a sclerotized band. The proximal arm of this band points to a small triangular sclerite, on the posterior-mesial surface of the cardo. The latter segment is rather membranous and appears to lie obliquely to the stipes, between the latter and the postgena.

Between the maxillae, on a line between the palpifers, is the spinneret. Since it points ventrally, it is not as apparent in this view as the sclerotized rings at its base. The lighter sclerotized ring completely surrounding the terminal part of the spinneret is the fusuliger. Lateral to it, sclerites of the palpiger can be seen running to the small pair of labial palps. The palps are anterior and lateral to the spinneret. The membranous area in front of the labial palps is the hypopharynx.

Posterior to the spinneret, between the dististipes, is a dark sclerite, the mentum. This envelopes the posterior portions of the spinneret, and lateral arms run anteriorly on either side of the hypopharynx. The submentum is membranous and is just posterior to the mentum between the basistipes.

The Maxillae: The maxillae, Figs. 3F and 3G (stipes not shown), vary but little between instars in structure. The stipes, Fig. 2C, particularly the sclerotized portions, shows the most variation in respect to setal pattern. On the first and second instars there are two long setae on the stipes with a puncture between. A variable number of setae are located on the third and fourth instar stipes, but always more than two.

The punctures on the maxillae are constant in position and number. One puncture is found laterally on each of the two proximal segments of the maxillary palpus (mp). They are barely visible on Fig. 3F. Two puncture-like structures are located distally on the frontal surface of the third segment of the maxillary palpus, and proximally there is a sensory plate (sensillum placodeum pl. on Fig. 3F), which is just opposite the galea. The galea (ga) has a puncture on the ventral surface.

The Labium: The labium, Fig. 2D, although variable in size, does not differ in structure or setal pattern on any of the instars. The labial palps (lp) are distinctly three-segmented in most other lepidopterous larvae, but appear to be only two-segmented in *E. comyntas*. The basal segment of the labial palpus is roughly equal to the fusuliger (fg) of the spinneret in height. In most specimens it is one third and never more than one half

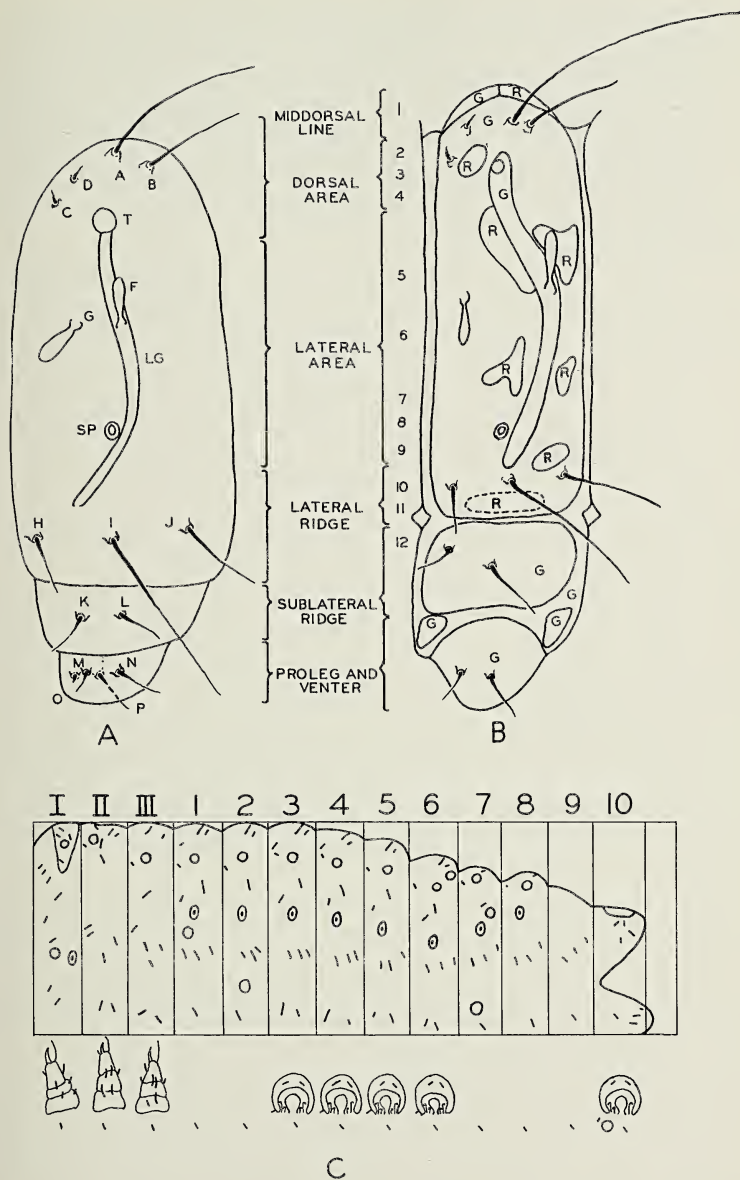


Fig. 6. A—B Diagrammatic drawings of the fourth abdominal segment of a first instar larva, left side: A. Position of setae and lenticles; LG=lateral groove (furrow), SP=spiracle. For explanation of other lettering see text. B. Color pattern; R=Red, G=Green; 1-12=areas of color. C. Setal map, left side of first instar larva; thoracic legs, prolegs and setae on the ventral side are shown at bottom of drawing.

the height of the fusulus (fs) as measured on its posterior aspect. The palpiger (pgr) bears no setae, but on the distal border of the mentum (mn) there is a pair of setae located one on either side of the spinneret. The two arms of the mentum extend alongside the paraglossae (me) anteriorly and then abruptly curve in a dorso-caudal direction. The paraglossa bears many spine-like processes which are somewhat larger than those on the hypopharynx (hp).

The Spinneret: The spinneret, Fig. 2D, is made up of an elongated fusulus (fs) and a wedge-shaped base called the fusuliger (fg). Except for a pair of punctures on its anterior surface the spinneret has no vestiture. The structure of the spinneret is the same in all instars. The measurements of the spinneret vary considerably within an instar, but the ratio between the length of the spinneret and labial palp fall in approximately the same numerical range in all instars, 2.3 to 3.4. Crumb (1929) found the spinneret varied considerably between genera of noctuid moths, particularly its relative length compared to the basal joint of the labial palp, as well as characters of the tip.

The Hypopharynx: The hypopharynx, Fig. 2D, forms the floor of the mouth and is flanked on either side by the fleshy lobes of the paraglossae (me). It begins as a raised, broad, flattened area anterior to the labial palpi. Its anterior spiny area in the mouth could be called a lingua, but posteriorly in the mouth cavity it narrows and forms a sort of trough between the paraglossal lobes. Small slender projections are sparse at the anterior and become more numerous posteriorly just before the trough. No noticeable differences occur in the hypopharynx between any of the instars.

BODY OF THE LARVA. *The Neck:* The neck is long and retractile into the prothorax. Except for a pair of cervical sclerites it is membranous. The sclerites (Fig. 8G) are located in the lateral areas of the anterior portion of the neck. There are only slight differences between the sclerites of individual instars except for gradual increase in size.

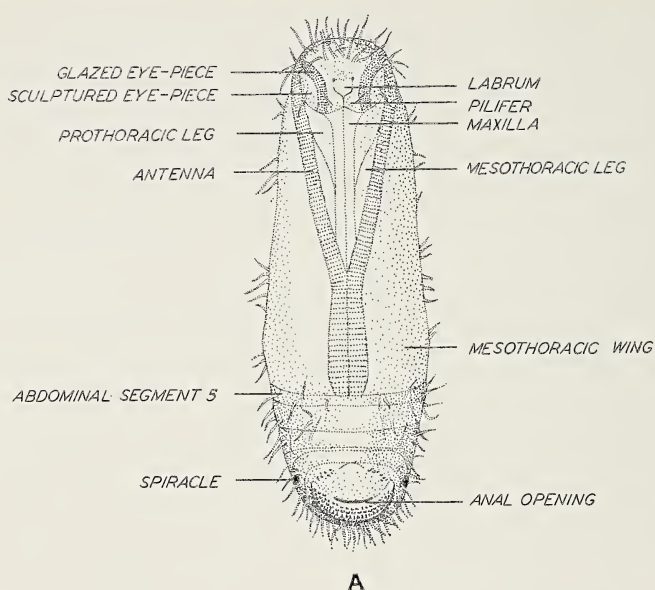
Setal Types: Four main types of setae were found on the first instar larva. The first type, here referred to as major setae, are all rather long, finely serrate, and have pointed tips. Examples of major setae are shown in Fig. 5O to 5R, and 5Y, and the location of specific setae on a particular segment is shown on Fig. 6A. All setae on the latter figure, and in the following discussion, are designated by letter. On Figure 6A, the following are major setae, A, B, H, I, J, K, L, M, N and P. Seta A on abdominal segment 4 was 258 microns in length.

Lesser setae, see Fig. 5S, are similar to the major setae structurally but differ in size; for example, D on abdominal segment 4 is 9.7 microns. A third type, here designated microscopic setae, are very minute and not easily seen. They are usually located anteriorly on each segment and are often hidden in the folds between segments. Seta C on the dorsum of the second abdominal segment measures 4 microns. Seta O is ventral in location and is the only other seta of this type given a letter symbol. No serious attempt was made to locate the microscopic setae on succeeding instars.

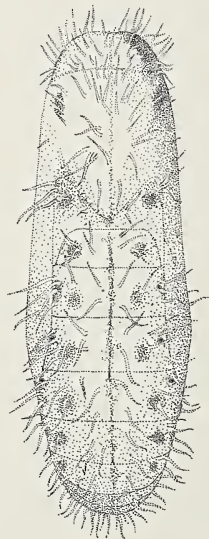
A fourth type of short stout setae is represented by setae G and F. These will be called pegged setae, see Fig. 5K to 5N. Both G and F are clavate and short. Seta G on abdominal segment 4 was found to be 29 microns.

Drawings of the longest major seta on the dorsum of the fourth abdominal segment on each instar and on the pupa are shown on Fig. 5O to 5R and 5Y. Here it can be noted that the only difference is a slight increase in diameter and length as follows: first instar, 258 microns; second instar, 343 microns; third instar, 386 microns; and fourth instar, 386 microns. In sharp contrast is the length of this seta on the pupa, 644 microns. The setigerous tubercle on the pupa (Fig. 5Y) is always smooth and wider than tall. Contrary to what might be expected these setae are not proportionally larger with each succeeding instar as is the case with the spiracles on the larvae, which roughly follow a geometric progression in size with each succeeding instar. A pointed projection is sometimes found on the side of the setigerous tubercle of the larvae, giving the prominence a starlike appearance from above. Little correlation could be noted with presence or absence of these projections on the tubercles and particular types of setae (except in the spiculate setae discussed below); for instance, the tubercles of 5L and 5M and 5Q and 5R.

Many pegged setae are present on the second instar. They tend to be concentrated in the lateral area of all segments though in no recognizable or consistent pattern. Their setigerous tubercles have either one pointed projection or none. Fig. 5L shows one of these setae on the fourth abdominal segment. Its length is 48.4 microns. Similar setae are found on the third and fourth instars but the number of projections on most of the setigerous tubercles is four or more. These pegged setae on the third instar are merely blunt at the end rather than clavate. Fig. 5M shows one of this type on abdominal segment 4, which measures 71 microns. Similar types on the fourth instar are more pointed.



B



C

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Fig. 7. A—C. Pupa, showing setal pattern and sclerites; A. Ventral view. B. Lateral view. C. Dorsal view.

Fig. 5N shows one on the fourth abdominal segment which measures 100 microns. No pegged setae were found on the pupa.

A fifth setal type here called a spiculate seta (Fig. 5T to 5W) is not found on the first instar. It differs from the other types in that tiny spicule-like projections occur on the distal third of the seta. At low magnification these distal projections give the impression of pine trees, see Fig. 8I and 8J. Spiculate setae on the second, third, and fourth instar larvae have the same length and apparently the same number of spicule-like projections. Spiculate setae on the second instar are located only near the honey gland. Those on the fourth instar differ in that their setigerous tubercles have pointed projections, whereas the setigerous tubercles of the second instar spiculate setae are smooth. The fourth instar larvae has spiculate setae on other areas of the body in addition to their normal position. On one specimen they occurred near the second abdominal spiracle and on another they were near the first abdominal spiracle. Length measurements in instars 2 to 4 are: 101.3, 103.3, and 93.6 microns respectively. Measurement of a spiculate seta on the pupa is 116.3 microns. Again it can be seen that size of a particular type of seta could not be correlated with the increase of size of other structures in succeeding instars.

From the above discussion of setae, it can be judged that there is considerable variation in number, kinds, size, and location of these structures from one instar to the next. In addition, there is variation in setal pattern (except in first instar larvae) between different individuals in the same instar. The short more or less clavate setae are the most variable in position, but the spiculate setae, though often found near the honey gland, may also occur on other areas of the body.

Setal Map of the First Instar Larva: The body of the larva is covered by many tubercles, each of which may or may not bear a single seta. Tubercles not bearing setae are here called lenticles, and when the word seta is used the fact that it is in all cases borne on a tubercle is understood. Certain of the setae and lenticles show a definite pattern of arrangement on all instars. The pattern is best seen on the body of the first instar larva (Figs. 1C, 1D) and is indicated on the setal maps (Figs. 6A, 6C). The extreme "hairiness" of the later instars makes setal maps impractical.

The map (Fig. 6C) shows the left side of a first instar larva. Roman numerals designate thoracic segments, and arabic numerals the abdominal segments. Large circles represent lenticles

and short lines represent setae. The left thoracic legs are shown below the map from a medio-ventral view, and the prolegs from a ventral view. A prothoracic shield on the dorsum of the prothorax and an anal plate on the dorsum of the ninth and tenth abdominal segments are indicated on the map. Figure 6A is an enlarged partially schematic view of the fourth abdominal segment. Setae are indicated by letters of the alphabet. Setae on other segments are given the same letter as those on the fourth abdominal segment having a similar position. Not all setae could be designated in this manner, especially those of the prothorax and the ninth and tenth segments.

A furrow (LG, Fig. 6A), is present on each segment starting on the dorsum and passing posterior to the edge of the dorsal lenticle and just posterior to the spiracle and ending in the vicinity of the lateral ridge. This furrow varies only slightly from segment to segment. Although it is a convenient landmark, the furrow is not shown on the setal map, Fig. 6C.

In plotting a setal map, the rectangles are drawn first, and setae and lenticles are then added. For convenience, the rectangles are made equal in size, with the result that horizontal distances are sometimes not in proper proportion. This would occur when some segments, for example, the prothorax, is much wider than another segment. Its setae would nonetheless be placed in the same horizontal distance as a subequal segment. Vertical distance, on the other hand, is easier to indicate on the map, and except for slight distortion of spatial relationship at the dorsal surface (top of the rectangle), the setae are in their proper relative positions.

Except for the prothorax all segments of a first instar larva are about equal in width (see Fig. 1C, 1D). All segments from the mesothoracic to the third abdominal segment are roughly the same height. Although somewhat schematic, Figure 3K gives the cross-sectional shape of the first instar larvae.

Terminology used to designate setae and their location is partially that of Clark and Dickson (1956). The reader is referred to the typical segment drawn on Fig. 6A, where the following main regions are labeled. Some of the regions, i.e., the lateral ridge, might be more distinctive in Fig. 3K. The area between the mid-dorsal line and the lower edge of lenticle T is called the *dorsal area*. That between the lower edge of the spiracle and lenticle T is referred to as the *lateral area*. The ridge below the spiracle is called the *lateral ridge* and the ridge below this is called the *sublateral ridge*. The leg or proleg is below

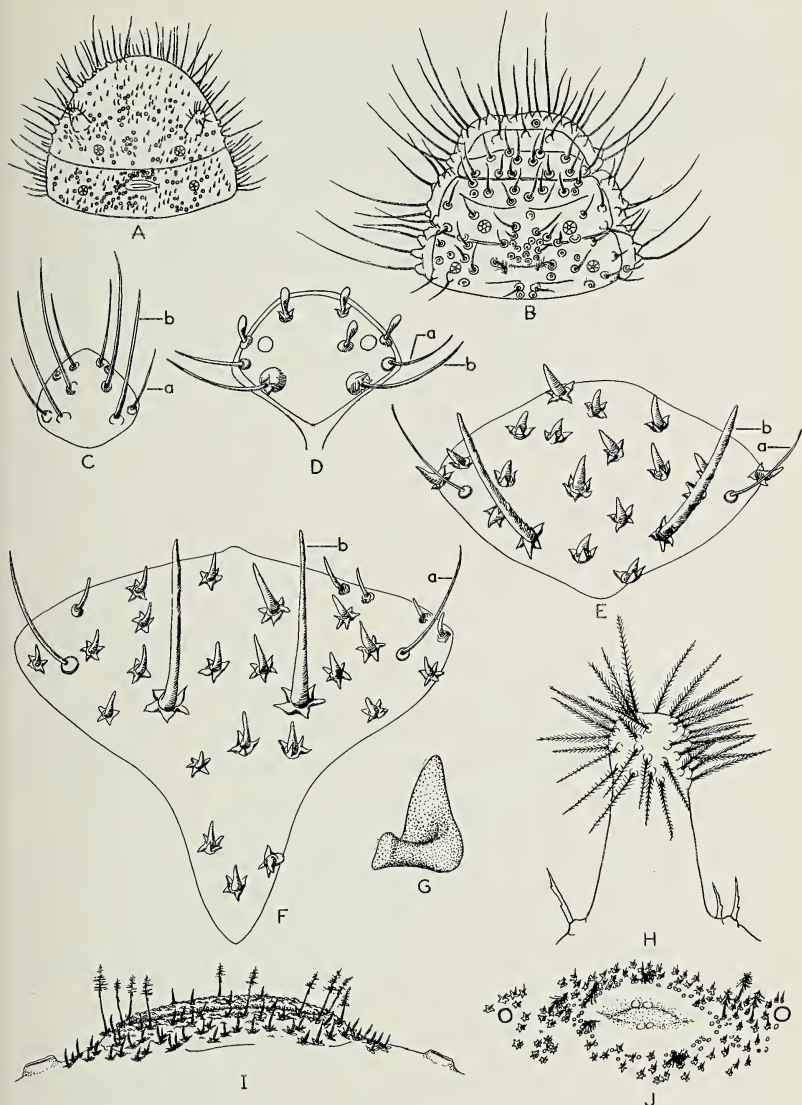


Fig. 8. A—B Dorsal view of honey gland and eversible tubercles; A. Abdominal segments 7, 8, and 9 in fourth instar larva, showing position of organs in relation to each other and spiracles. B. Same, second instar larvae. C—F. Dorsal view of prothoracic shield of first (C), second (D), third (E) and fourth instar larvae. Setae *a* and *b* can be traced ontogenetically by structures at their base (see text). G. Cervical sclerite, 3rd instar larva. H. Lateral view of extended eversible tubercle from fourth instar larvae. I. Partially schematic anterior view of honey gland of fourth instar larva. Clusters of spiculate setae are prominent around the gland; the inverted tubercles on segment 8 appear on each side. J. Dorsal view of same.

the sublateral ridge. Where neither proleg nor leg occur on a segment, the area below the sublateral ridge is called the venter.

The following section is a description of the specific setae and lenticles on each segment of the first instar larvae and on the prolegs. Only the setae for the left half of the larvae are mentioned. Later instars are not treated in as much detail as the first.

Prothorax: A prothoracic shield, Figs. 8C to 8F, is located on the dorsum of the prothorax. It is roughly diamond-shaped with the anterior corner being so rounded as to make the anterior half approach a semicircle in shape. A major seta is located near the anterior corner just to the left of the mid-dorsal line on the shield. Slightly posterior and somewhat ventral to this seta is a lenticle lying just inside the margin of the shield. Posterior to and above the lenticle is another major seta. On the posterior half of the shield are located two more setae; the first on the posterior margin of the shield near the lateral corner and the second dorsal and slightly posterior to the first. The ontogeny of certain structures on the shield is discussed below.

The bases of four setae on the lateral surface of the prothorax describe a diagonal line parallel to the anterior margin of the shield. The most posterior of the group is located just below the lateral corner of the prothoracic shield. Two other setae together with a lenticle and the prothoracic spiracle respectively describe another diagonal on the lateral ridge with the spiracle near the intersegmental line. Two more setae, one anterior and dorsal, the other posterior and ventral, are located on the sublateral ridge. These have been designated K and L respectively and both occur also on the other thoracic segments and on abdominal segments 3, 4, 5 and 6. Near the midventral line is a seta here called P that is repeated on all segments. This occurs on every thoracic and abdominal segment and is indicated by the lowest setal symbol on the map Fig. 6A.

Mesothorax: Six dorsal setae and a lenticle are present. Just to the side of the mid-dorsal line on the anterior third of the segment is a major seta and ventral to this a lenticle called T. A lenticle in roughly this same relative position is found on the metathorax and the first eight abdominal segments. A microscopic seta C is found anterior and slightly ventral to this lenticle and varies in position vertically up and down in front of the lenticle on the metathoracic and first eight abdominal segments. In a ventral and slightly posterior position is found another major dorsal seta. Posterior to the intrasegmental furrow

and midway between the lenticle and dorsal midline are two more major setae. The anterior one is called A and the posterior B. This pair of setae is found to be present on the metathorax and first six abdominal segments. A group of four setae is found on the lateral ridge. Setae K, L, and P, are also present.

Metathorax: Setae A, B, C, K, L, and P, and lenticle T are present. A pegged seta G is found midway between the lenticle and the lateral ridge. Four other setae are present on the lateral ridge.

Abdomen: First Segment. Setae A, B, C, G, L, and P, and lenticle T are present. A lesser seta called D is found just dorsal to C. Anterior to the furrow and situated midway between the dorsal lenticle and the spiracle is a pair of pegged setae. The anterior is G, and the posterior, F. Both are found together on the first six abdominal segments, and on other segments F appears to be in the furrow. A lenticle is present below and just anterior to the spiracle and not quite on the lateral ridge. The three setae present on the ridge are designated from the most posterior as H, I, and J. This group is found on the first nine abdominal segments.

Second Segment. Setae A, B, C, F, G, H, I, J, and P are present in their normal positions. A lenticle is present dorsal to, and somewhat posterior of, seta L, which is the only seta on the sublateral ridge. Seta D could not be found.

Third Segment. Setae A, B, C, D, F, G, H, I, J, K, and P are present in their normal positions though C is dorsal as well as anterior to lenticle T. Three major setae are present on the proleg; an anterior lateral seta called M, a posterior lateral seta called N, and on the medial side of the proleg a seta P. A microscopic seta (O) is located in an anterior position on the medial surface of the proleg. The setal pattern on the other prolegs is the same except that O could not be located on the anal proleg.

Fourth Segment. All setae found on abdominal segment 3 are found on abdominal segment 4 in identical positions.

Fifth Segment. Other than D, which could not be found on this segment, and the fact that C is directly anterior to lenticle T instead of dorsal, this segment is identical in vestiture to abdominal segment 4.

Sixth Segment. A lenticle called S located dorsal and posterior to lenticle T makes its appearance on this segment. In other respects the segment is identical in vestiture to abdominal segment 4.

Seventh Segment. Lenticle S is located dorsal and anterior to lenticle T on a vertical line with the spiracle. Both lenticles are posterior to the furrow. K is absent. A lenticle occurs on the sub-lateral ridge. Setae O and F are present but the proleg setae M and N are not. Setae B and G are not present, but the remaining setae are as on segment 4.

Eighth Segment. Lenticle S is the only lenticle present. Present are seta A, C, H, I, J, L and P only.

Ninth Segment. Setae H, I, J, L, O and P are the only setae to be found on this segment. No spiracle or lenticle is present.

Tenth Segment. Four setae possibly "homotypic" with A, H, I, and J are located in a dorso-lateral position above the anal line. Four setae (undesignated) are located below the anus and above the anal proleg. Setae M, N, and P are present on the proleg. Two setae and a lenticle in addition are located anteriorly on the mesial surface of the proleg. A somewhat rounded rectangular anal plate makes its appearance on the dorsum.

Comparison with Other Lycaenid Larvae: Setal maps of *E. comyntas* and *Plebejus (Icaricia) icarioides* Bdv. were compared to see if there were any consistent differences. The purpose of this comparison was not only to discriminate the two species but possibly to gain some insight into generic differences in the immatures. The taxonomy of the above species was originally derived by use of adult characters.

The vestiture of the legs, prolegs, and prothoracic shield did not differ. The following is a summary of differences between the first instar larvae:

Present in *E. comyntas* and absent in *P. icarioides*: Seta D on the sixth abdominal segment and lenticle 7 on the seventh abdominal segment. Structures present in *P. icarioides* and absent in *E. comyntas*: Setae K and F on the mesothorax; seta G on the seventh segment and lenticle S on abdominal segments 1, 2, 3, 4, and 5.

With the limited material on hand (cast skins only), it was possible to make maps of only the first six abdominal segments of the first instar larva of *Plebejus (Lycaeides) melissa* Edw. There was nothing on the specimens examined to suggest that they were different from *P. icarioides*.

A first instar larva of *Strymon melinus* Hub. differs from both *Everes* and *Plebejus*. Setae G and F are not clavate in the former species and dorsal lenticles S and T are very close together. A lenticle is present between K and L on abdominal segments 3, 4, 5, and 6, while no lenticles are found in these locations on

E. comyntas, *P. icarioides* or *P. melissa*. The prothoracic shield of *S. melinus* differs in that it bears an extra pair of setae. The anal plate is longer than wide, roughly oval in shape (with the broader portion anterior) and has two punctures on the posterior half.

Prothoracic Shield: The setae on the shield of the first instar have been described and figured (8C). The shield is defined on the second instar by a line, apparently a suture, enclosing a smooth green area. In contrast the surrounding area is granulated. The suture is less easily observed on the third and fourth instars, but the parts of it that are distinguishable enclose the area which, though green and therefore distinguishable on the living specimen, is granulated like the surrounding skin. Whereas the prothoracic shields of the first instar larvae of *E. comyntas* and *P. icarioides* are relatively similar, later instars of the two species seem to differ more markedly. Other species, for example *S. melinus*, bear additional setae on this structure in the first instar. It is presumed that the prothoracic shield may be of some interspecific taxonomic importance.

In spite of the great increase in the number of structures on the prothoracic shield in later instars (see Fig. 8D-8F), some setae can be traced ontogenetically. This can be done partly by position and setal type, but also by structures at the base of the setae. The most posterior-lateral setae on each side of the first instar shield are each located on a distinct sclerotized area, the pinaculum. The latter are slightly larger than the base of a typical seta which elevation (tubercle) could be termed a papilla. The papillae are also present on these setae, marked "a" in Figure 8C to 8F. These very slender long setae represent a type not seen elsewhere on the larvae, even though it falls into a major setal category on the basis of its length. Another pair of setae, marked "b" in Figs. 8C to 8F, are more mesial on the shield, and are located on a prominence called a chalaza. The chalaza-borne setae "b" can be easily traced in the drawings. Mackay (1959) also found that the bases of the setae were useful in identifying particular setae in the Olethreutidae.

The second instar prothoracic shield bears a pair of lenticles which are "homologous" to those on the first instar. They are in a somewhat similar location. These lenticles may or may not appear on the third or fourth instar, and their position may also vary.

Clavate, blunt, or pointed pegged setae occur on the second, third, and fourth instar shields and are variable in number and position.

Blackish areas may be present on the shield. Some first instar larvae had a pair of blackish spots along a longitudinal line posterior to each of the lenticles, others had a posterior pair of wedge-shaped blackish areas on each side of the mid-dorsal line. These areas were also noted in second and third instar larvae. On others the entire prothoracic shield was green.

Anal Plate: The anal plate is located in the center of the dorsum on the tenth abdominal segment in first instar larvae. It is square in shape with rounded corners. The sides of the plate are approximately equal to one third the width of the segment. The plate is devoid of setae and is not granulated, but on one specimen a minute lenticle (or puncture) was seen on each lateral edge of the plate. The plate did not occur on later instars.

The anal plate of *E. comyntas* tended to approach a square in shape, while the anal plate of *P. icarioides* was hexagonal, being somewhat wider than long. This suggests that there may be some taxonomic usefulness in this structure.

Legs: According to Fracker (1915) "No one has yet discovered characters of much value in the structure of the thoracic legs, so uniform are they throughout the entire order." Comparison of the prothoracic leg of *E. comyntas* with the prothoracic leg of a larva of *Cirphis unipuncta* (Haworth) (drawing in Ripley, 1923) shows no significant difference in structure or setal pattern. Figures 5E to 5J, show the thoracic legs in the first instar larvae. No consistent difference between instars was noted.

Prolegs: There are five pairs of prolegs. Those located on segments 3, 4, 5 and 6 are referred to as the ventral prolegs and those on the last segment as the anal prolegs. Each proleg has a biordinal mesoseries of crochets interrupted in the middle by a fleshy spatulate lobe, see Figures 5A to 5D. This arrangement is diagnostic of the family Lycaenidae. There is generally the same number of crochets on each side of the lobe in each instar. The average number of crochets on the proleg of the first instar is four (Fig. 5A); on the second, seven; on the third, fifteen; and on the fourth, twenty-three. The relationship between the fleshy lobe and the crochets in the fourth instar proleg is given in two views, Figure 5C and 5D.

The number of crochets per proleg is constant on the first instar larva, there being four on each ventral proleg and three on each of the anal prolegs (Fig. 5B). In later instars the number is subject to some variation between individuals of a given instar and even between members of a proleg pair. The average number for an instar, however, appears to remain fairly constant.

Lenticles and setae occur on the medial surface of the prolegs as well as on the lateral surface. The medial surfaces of the anal prolegs and of the fourth abdominal proleg were studied on each instar. There is always one lenticle on the medial surface of each anal proleg of the first and second instar larvae. (Fig. 5B). Two were found in this position on a third instar and three on a fourth instar. No lenticles occur on the medial surface of the fourth abdominal proleg of the first instar, however, two are present on the second and third instars and only one was found on a fourth instar specimen.

Setae on both surfaces of the prolegs become more numerous with each succeeding instar.

Honey Gland and Protrusible Tubercles: The honey gland and protrusible tubercles, see Fig. 8A, B, I, J, are found only in the later instars. Though the second instar larva does not have the tubercles, it does have a functional honey gland on the dorsum of the seventh abdominal segment (Fig. 8b). On the third and fourth instars in addition to the honey gland a pair of protrusible sacs or tubercles (Fig. 8H) are located posterior and somewhat lateral to the eighth abdominal spiracles (Fig. 8A). A spiculate seta is located on each of the lateral margins of the gland on the second instar. Along the posterior margin of the glandular orifice is a cluster of lenticles with no definite arrangement. The anterior margin does not bear setae or lenticles. The gland on the third instar has the same vestiture except the lenticles are more numerous and there are three spiculate setae at each of the lateral margins of the gland. Although there are more of these setae on the fourth instar honey gland, they are not arranged with an equal number on each side. For example, one specimen has four on one side and eight on the other.

When the protrusible tubercles on the third and fourth instar are extended, they can be seen to bear spiculate setae (Fig. 8H) on their distal parts. These setae are unlike other spiculate setae in that the spicules are shorter and are proximal as well as distal in position. When the tubercles are only part way protruded, the setae can be seen grouped in a vertical bundle in the center of the tubercle. When fully protruded the setae point in all directions. The tubercle is often fluttered up and down between these two positions making the setae appear to move by their own power. A count was made of the number of spiculate setae per tubercle on fourth instar larvae: They vary in number from 29 to 34 and may also be variable in numbers between members of pairs on one individual. The third instar seta measured 76 mi-

crons and the fourth instar about 112 microns. Other measurements of the gland and tubercles are given in Table 1.

Coloration: Three basic colors, brown, green and black, make up the color pattern of the larva. Black color, which is probably due to pigments in areas underneath transparent epidermis is found only on the prothorax. On the first instar larva this color was seen just anterior to the prothoracic spiracle in a depression above the lateral ridge. The border of the prothoracic shield and certain spots on the shield also showed this color.

When viewed from the side the larva appears to have at least twelve longitudinal alternating light green and brown areas. In gross examination these areas are not all obvious, so that the larvae may appear to have only a few anterior to posterior color stripes. When viewed under a microscope these appear as a linear arrangement of small pigmented patches. The larvae, however, are described in the following paragraphs as if the areas were not broken up into pigment patches. The fourth abdominal segment of a first instar larva is shown in detail in Fig. 6B to illustrate longitudinal areas of color. They have been numbered from one to twelve for ease in discussion.

There is some variation in the color pattern, although its basic nature probably is fairly stable. For instance, the lighter stripe marked by number two, in a particular premolt fourth instar larva was nearly obliterated by the enlargement of stripes one and three; ordinarily the stripe is well defined in a freshly molted fourth instar larva. It is possible that some color changes are due to increasing pigmentation during a particular instar. Variations in which the larva has dark green areas instead of brown or reddish-brown are about equally common and occur in siblings from the same female.

First Instar Larvae: Mid-dorsal Line. — This line (marked 1 in Fig. 6B) is dark brown and extends from the dorsum of the mesothroax to the dorsum of the ninth abdominal segment where the line broadens to cover most of the dorsal area. The tenth segment bears five alternating light green and dark brown transverse bands, the most anterior being light green.

Dorsolateral Area. — A broad light green stripe makes up this area extending from the prothroacic shield to the tenth abdominal segment. There is a hint of a fine dark brown stripe extending within the light green one, from abdominal segment 4, passing just dorsal to the lenticles and merging with the mid-dorsal line on abdominal segment 7.

Lateral Area. — This area is basically made up of five alternat-

TABLE 1

Measurements (in mm.) of the honey gland and eversible tubercle in larvae of *Everes comyntas* Godt.

Instar	No. Exam.	Gland Orifice Length	Gland Length	Gland Width	Tubercle Height	Diameter of base Extended Tubercle	Diameter of base Retracted Tubercle
4	5	256-372	370-549	204-256	255-362	155	154-179
3	5	154-256	282-384	128-204	155	--	77-128
2	5	102-154	256	102-128	-	--	--

ing reddish-brown and light green stripes extending the length of the body. The first of these lateral stripes (5) going in descending order is reddish-brown and starting just below the prothoracic shield it runs as far as the tenth abdominal segment where it merges with the last dark transverse band mentioned under the section on the mid-dorsal line. The second stripe (6) is light green and extends from the prothorax to the sixth abdominal segment. It is represented as haloes around the seventh and eighth abdominal spiracles and as small squarish patches on the ninth and tenth abdominal segments, the haloes and patches both being bordered by the merging first and third reddish-brown stripes. The third stripe (7) is dark colored and starts as a fine line just on the posterior edge of the prothorax and extends back to the eighth abdominal segment where it

merges with the first and fifth dark reddish-brown stripes. The fourth stripe (8) is a broad light green band extending from the prothorax, where it merges with the light green stripe on the lateral ridge, to the fourth abdominal segment. It is represented by haloes around the fifth and sixth abdominal spiracles. The fifth stripe (9) is reddish-brown and extends from the mesothorax to the fourth abdominal segment where it becomes obscure.

Lateral Ridge. — The entire lateral ridge is light green except on the underside of the last four segments where it is dark brown.

Sublateral Ridge, Venter, And Prolegs. — These areas are entirely light green in color.

Second Instar Larvae. The second instar has the same basic pattern as the first instar with the following exceptions: Stripe number three begins on the mesothorax and ends on abdominal segment 6, the honey gland being light green in color is in this area. An area between the prothoracic shield and lateral ridge is reddish-brown except for a small light green stripe in the middle. Stripe number eleven extends from the second abdominal segment to the anus.

Third Instar Larvae. The color pattern is the same as in the second instar.

Fourth Instar Larvae. Same coloration as third instar only the dark stripes are broader and darker brown and the light stripes are greener. Other differences are as follows: Stripes number one and three nearly merge and the only remnant of stripe number eight is found as haloes around the spiracles. Stripe number eleven under the lateral ridge merges with stripe number twelve on the sublateral ridge which is also brown. Together they extend the length of the larva.

In addition to the above the lateral sides of the ventral prolegs are reddish-brown, the remainder being green. The entire anal proleg is reddish-brown. The venter is green.

THE PUPA

The obtect pupa of *Everes comyntas* is long and slender: average length of specimens examined was 6.7 mm.; average width at the widest portion was 2.5 mm. Thus the pupae are about three times as long as broad (not 4 to 1 as indicated by Scudder, 1889, vol. 3, p. 907). The ratio agrees with the length and breadth of the three European species of *Everes* figured by Lorkovic (1938). The average height at the highest point (3rd or 4th abdominal segment) was 2.4 mm.

The small size of the pupa, its slender profile, and the numerous long setae are fairly indicative of this species. These fea-

tures are shown on Figure 7 a, b, c. The living specimen is whitish-green in color, with the head and thorax tending to be slightly darker green than the abdomen. A conspicuous mid-dorsal black line, while variable between individuals, extends from the prothorax to the seventh abdominal segment, where it fades out. The lateral and dorsal surface is speckled with many small dark brown to black spots. A lateral row of larger spots is also present just dorsal and slightly posterior to each abdominal spiracle. A larger spot occurs in a similar position on abdominal segment one, a slightly smaller spot on the metathorax and a still smaller dark area occurs on the mesothorax just posterior to the spiracle.

Reddish marks may be present in some individuals on both sides of the lateral lines on the abdomen.

Setae, Hooks, and Papillae. The major setae are basically white in color, so that as one observes a pupa he notes first its greenish color and shape and is subsequently cognizant of numerous long setae on the dorsal and lateral surface. These setae have been stippled on the drawing on Figure 7 in hopes that their unobtrusive nature may be imparted. In addition to the completely white setae, some are colored with one or more dark brown or black bands variously located at the base, tip or intermediate positions.

Most of the setae on the pupae are major setae, but a few on the venter of the abdomen are small in comparison with the others. The size of the smallest on one specimen was 43 microns. Since there was a difference in number between groups of setae on one side and the corresponding groups on the other, and between individuals, the taxonomic value of setae numbers is vague.

Spiculate setae are found on the prothorax and sixth abdominal segment only. They are one third to one quarter the size of the major setae covering most of the pupa. Those on the prothorax were not constant in number although they do occupy the same general position on most specimens. Those on the sixth segment are more constant in number and position. Commonly there are two spiculate setae located dorsally and slightly posterior to the sixth abdominal spiracle although sometimes there may be one or none.

A group of cremastral hooks is found near the anal opening on the tenth abdominal segment. Those measured range in size from 48.5 to 70.5 microns. They are variable in number and position but are prominently clustered in a "C" shaped band around the posterior part of the anal slit.

Although the pigment spots in some individuals are suggestive of a roughened surface, no papillae were noted on the pupae which were not associated with setae.

THE HEAD. *Vertex:* Perhaps the most difficult of the head structures to locate is the vertex, which is reduced to two small triangular sclerites. These lie on either side of the dorsal midline just anterior to the prothorax and just posterior to the bases of the antennae. The vertex lacks both setae and papillae. Its position and its small size preclude its being shown on Fig. 7A or 7B.

Front, Clypeus, Labrum: There is no fronto-clypeal or clypeo-labral suture, which makes the boundaries of these particular areas obscure. Two pores, representing the anterior tentorial pits, are usually apparent between the eyes. Arms of the "U-shaped" suture demarking the limits of the labrum point to the tentorial pits. Since the pits are associated with the lateral margins of the clypeo-labral suture in other insects, we may assume the area between and cephalad of the pits to be the clypeus, which is not distinct from the frons to which the antennae are attached. Below the pits, the labrum is distinct. The region between clypeus and glazed eye-piece is the gena.

The pilifers, caudo-lateral projections of the labrum, are enlarged and in most individuals, meet in the midline caudad of the labrum proper.

Labial Palps: In a few individuals, a small triangular portion of the labial palpi separates the lobes of the pilifers. The external appearance of the labial palps between the pilifers is thus variable in individuals of *comyntas*. The palpi also vary in expression in other species. In *Atlides halesus*, for example, the pilifers touch and the labial palpi can only be seen between the proximal bases of the maxillae.

Maxillae: The maxillae are very prominent just laterad of the mid-line between the pilifers and the central junction of the two antennae. They are only slightly longer than the length of the united distal parts of the antennae (see Fig. 7A).

Eye-pieces: Between the labrum and the antennae are the prominent eye-pieces; a lunate mesal portion has a smooth glassy surface and lacks setae; the lateral sculptured eye-piece has the same texture as the gena.

Antennae: The distal one-third of the antennae are united in the midline. Externally the clavate ends of the antennae appear to stop at the fifth abdominal segment, as do the wings. However, there is a small oblique pocket beneath the fifth segment,

into which the tips of the antennae (usually less than 2.0 mm.) fit comfortably. This is best observed in specimens preserved in fluid in which the intersegmental area might be slightly distended due to swelling.

THE THORAX. Thoracic segments are indicated in Figures 7B and 7C. They are similar to other lycaenid pupae in general shape. Proportionate lengths along mid-dorsal line are: prothorax, 2.5; mesothorax, 7.0; metathorax, 1. The mesothoracic spiracle is level with the surface, is not associated with prominences or tubercles and appears plugged with a narrow, highly reticulate cover.

A group of 6 to 8 small pores is found on the distal surface of the mesothoracic leg. Lesser numbers occur in the same position on the prothoracic leg. These openings may vary in number on each side of the body and between individuals, but they are always present. Other species of Lyaenidae also have these pores. They are of unknown function.

THE ABDOMEN. *Honey Gland Scar and Tubercles:* The honey gland scar is located on the dorsum of the seventh abdominal segment in the same position as on the larva. It is more prominent on some specimens when it is pigmented, but it is very difficult to detect in others. Though in other Lycaenidae the pupal honey gland is functional, it is not functional in *E. comyntas*. No markings or scars indicative of the protrusible tubercles could be found on segment eight.

Stridulation: As most lycaenids, *comyntas* pupae are able to stridulate. The noises produced are barely audible and can be best described as slight chirping or squeaking sounds. It is best to place the pupae in a vial or other reflective container in order to hear the sounds.

These organs were first reported in *comyntas* by Downey and Strawn (1963) and Strawn (1964). Downey (1966) subsequently noted the stridulatory organs in pupae of the Palearctic *E. argiades* Pall.

The sound-producing structures are located on the inter-segmental membrane between abdominal segments 5 and 6. To function, a posterior file containing numerous teeth is grated across an anterior stridulating plate. A recurved region of membranous folds lies between the grating surfaces.

Stridulating plate: A narrow (0.05 mm.) band on the dorsal posterior membrane of segment five extending laterally to, or just lateral of, the spiracle. The surface is of grainy texture, with the main axis of the "grains" in a transverse row. Each "grain"

has one or more small tubercles whose delineation makes more apparent the region of the stridulating plate. The latter is not sclerotized as it is in many other species so that the plate in *comyntas* is defined mostly by its roughened grainy surface. The tubercles range in height from 2 to 5 microns and vary slightly in number and position upon the plate.

Intersegmental fold: This area of the intersegmental membrane is identified by its position and its lack of any sclerotized structure. It is in this region that the membrane folds back on itself so that the anterior plate is in juxtaposition with the posterior file. Two relatively narrow longitudinal muscles are attached by means of short ligaments to the membrane. These attachments are in a dorso-lateral area, midway between the spiracular and the mid-dorsal line. Contraction of the muscles pulls the membrane and produces the grating action of the file against the plate.

File: This area is defined in *comyntas* solely on the presence of teeth. The latter are small, unsclerotized, indistinct protuberances which show a tendency for clustering. The same type of teeth, not quite as numerous, occur in other intersegmental membranes, and also on exposed portions of the pupal integument where they do not contact other surfaces. However, this situation prevails in pupae of over 100 other lycaenid species examined by Downey, and there seems to be little doubt that, in the region of the stridulating plate, the teeth serve as frictional devices in sound production.

The file extends laterally a greater distance than the stridulating plate.

DEHISCENCE. Emergence of the adult is accomplished by a mid-dorsal split of the thoracic segments. As the adult exits through this longitudinal split, it forces the lips apart. This splitting progresses posteriorly along the seam between the wings and the abdomen. Frequently ruptures also occur between the prothorax (to which the vertex usually remains attached) and the antennae, progressing for a variable distance along the antennal suture down the ventral face. The face covering, however, remains attached to the pupal skin. A gradual darkening of the pupae occurs about 48 hours prior to eclosion.

SUMMARY AND CONCLUSIONS

The external morphology of the immature stages of *Everes comyntas* is described and treated in some detail. This includes the egg, head capsules of the various instars, mouth-parts, setal pattern, honey gland, and characters of the pupa.

Different types of setae not previously known for this species are drawn and described.

Variation is found in number and position of the setae on the head and body between individuals of the same instar (except first instar larvae) and between individuals of different instars. Other characters showing variation include depth of the labral notch, segmental ratios of the antennae between instars, setal lengths, morphological structure of the setae, number of crochets, and coloration.

Individual variation is found in the following characters: setal pattern; presence or absence of spiculate setae; presence or absence of the honey gland scar; number size, and position of cremasteral hooks and coloration.

Because of this extreme variation it is suggested that those involved in a comparative description of immature Lepidoptera make a study which is not only thorough in detail but which includes examination of a large number of specimens of all instars.

The honey gland is described on the second, third, and fourth instar larvae, and the scar is noted on the pupa. Eversible tubercles on the third and fourth instar larvae and a pupal stridulating device are described.

A complete setal map of the larva is plotted. Comparison of a first instar setal map of *E. comyntas* with one of *P. icarioides* shows that, though similar in many respects, there are decided differences in presence and absence of seta and lenticles. The usefulness of setal maps of butterfly larvae is demonstrated and should point the way to more work of this type.

Some differences in the prothoracic and anal plates of several lycaenid species are pointed out which suggest that these structures may be of importance in the taxonomy of the larvae of Lycaenidae.

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A LITTLE-RECOGNISED SPECIES OF *HELICONIUS* BUTTERFLY

(*NYMPHALIDAE*)^{1,2}

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THE TAXONOMY OF THE SOUTH AMERICAN butterfly genus *Heliconius* (Nymphalidae) Kluk is in confusion, not because the species are "critical" as a result of inbreeding, apomixis or other evolutionary processes incompatible with the rigid species concepts inherited from the theory of special creation, but simply because the species are polymorphic, show remarkable geographical variation, and mimic each other; thus as Fox (1956) has said of another South American group, the Ithomiidae, two apparently identical butterflies may belong to distantly related species, while two having hardly a single pattern in common may be conspecific.

While studying geographical variation and mimicry in the genus (See Turner 1963b, 1965 for preliminary summaries) I find it necessary to give a definition of *Heliconius elevatus* Nöldner, a species which has seldom been properly recognised, and to describe a new subspecies.

The species *H. elevatus* shows strong geographical variation, each form resembling very closely a form of *Heliconius melpomene* (Linnaeus), a highly variable species which shows both geographical variation and polymorphism (Turner & Crane 1962; Sheppard 1963; Turner 1965); as a result the two species are usually confused in various ways. Neustetter (1929) came near to the truth in separating several forms of *elevatus* as a species different from *melpomene*, but spoiled the result by splitting *melpomene* itself into several species, and including two of the *elevatus* subspecies with *melpomene*. Eltringham (1917) was firm about the separation of *elevatus* from *melpomene*, although he regarded *tumatumari* Kaye, here listed as a subspecies of *elevatus*, as a species in its own right. Oberthür (1916) correctly regarded *tumatumari* as a form of his own *bari* and separate from *melpomene*. In other works (e.g. Emsley 1964) and in most collections, *melpomene* and *elevatus* are confused. The latest revision

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²This paper is dedicated to the team working on the biology of Heliconiinae at the William Beebe Station for Tropical Research, Trinidad, whose papers appear in the New York Zoological Society's journal *Zoologica*.

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Table 1
CONDITIONS FOR DYE-FEEDING

Breed No.	Colias Species	Dye (% of blend)	Feeding Start Length, mm	Time, day	Time Dye Fed, days	Pupation, day	Yield Pupae	Color Pupae
1	<u>surrythene</u>	none	-	-	-	23-31	(34 from 65 1st-instar larvae)	green
2	<u>surrythene</u>	Nile blue A (5)	22-24	20-21	1.5-1.8	22-27	10/10	one blue (15 mm), rest sl. blue-green at most
		neutral red (5)	19-24	17-21 ¹	5	23-26	7/9	pink (esp. on abdomen) to deep red
		Nile blue A (1) and neut. red (1)	22	21 ¹	3-5	24-26	5/5	green to green with blue abdomen
		brill. cre-syl blue (5)	18-20	21 ¹	4-5	25-26	3/3	green
3	<u>philodice</u>	Nile blue A (5)	15-23	14	0.8-1.4	18-19	4/20	blue-green ²
		Nile blue A (1)	24-27	16	2.3-4.5	20-22	2/8	greenish-blue; blue
		(1) neutral red (5)	15-19	14 ¹	4-5	18-19	7/10	dark-red
		(2) neutral red (5)	26-30	18	0.5	20-21	3/3	two dark-red; one green with red abdomen
		Nile blue A (1) and neut. red (1)	17-19	15	0.5	19	4/5	sl. blue tint
		brill. cre-syl blue (5)	18-19	15 ¹	3-4	18-19	4/4	sl. grayish green
4	<u>philodice</u>	neutral red (5)	28-32 (one at 24)	16-19 ¹	0-3	19-21	32/32	red to dark-red
5	<u>philodice</u>	Nile blue A (1)	27-30	16-17 ¹	2-3	18-20	4/10	blue-green

¹fed dye to pupation.²green for controls.

Fig. 1. Parallel variation of *H. elevatus* (left) and *H. melpomene* (right). Specimens of *H. elevatus* from the British Museum, (Natural History), of *H. melpomene* from the Hope Department of Entomology, Oxford (except). Colour: ground, dark brown to black; pale marks, yellow; dark marks, red. Left: A. *H. e. elevatus* ♂ Sao Paulo de Olivenca, upp. Amazons, August 1907 (M. de Mathan); B. *H. e. bari* ♂ Essequibo R., Brit. Guiana; C. *H. e. perchlorus* ♂, Mauchay, Beni R. viii 95 (Stuart); D. *H. e. tumatumari* ♀. Tiger Creek, Potaro R., Br. Guiana, May '07 (C. B. Roberts); E. *H. e. roraima* ♂, see type description; Right: F. *H. m. aglaope* ♂, "Tonantins, Amazon"; G. *H. m. thelxiope* ♂, Para, L. Amazon, iii — vi, 1915 (A. M. Moss, ex W. J. Kaye coll.); H. *H. m. vicinus* ♂, no data, ex coll. J. A. Gibbs, Keble college; I. *H. m. cybelele* ♂, Guyane francse. St. Jean de Maroni (coll. le Moul).



TABLE 2. DIFFERENCES BETWEEN H. ELEVATUS AND H. MELPOMENE

<u>elevatus</u>	<u>melpomene</u>
Male genital valves with a large strong hook and a marked tuft of hairs at the tip.	Male genital valves with weak hook near the tip, not accompanied by a marked tuft of hairs.
Anterior margin of hindwing with a red stripe on the underside	Anterior margin of hindwing with a yellow or red stripe on the underside.
A yellow stripe a few millimetres behind the anterior margin of the hindwing, underside.	A few millimetres behind the anterior margin of the hindwing' underside, either no stripe or a red stripe.
No prominent red spots at the base of the hindwing, underside.	Three to five deep red spots at the base of the hindwing, underside.
Often a row of marginal white spots on the hindwing, underside.	Seldom a row of marginal white spots on hindwing, underside.
Rays on hindwing, upperside, tend to be thick.	Rays on hindwing, upperside, tend to be thin.
Apical spots on forewing often present.	Yellow apical spots on forewing hardly ever present.
Often a yellow fleck at inner angle of forewing.	Never a yellow fleck at inner angle of forewing.
Yellow mark between veins M_3 and Cu_1 often with concavely indented distal border.	Yellow mark between veins M_3 and Cu_1 usually convex at its distal border.
Spots on head and palpi often white.	Spots on head and palpi often yellow.

of *Heliconius* separates some forms of *elevatus* but places two of the subspecies as hybrids between *H. melpomene* and *H. aoede* (Hübner); this revision (Emsley 1965) appeared while the present paper was in draft, and the evidence presented here is independent of Emsley's study; the general agreement of the two studies testifies to their correctness.

TABLE 3. NUMBERS OF GENITALIA EXAMINED

species	infraspecies	number
<u>melpomene</u>	<u>aglaope</u>	7
	<u>flavotenuiata</u>	0
	<u>thelxiope</u>	2
	<u>vicinus</u>	7
	<u>meriana</u>	0
	others	6
	total	22
<u>elevatus</u>	<u>elevatus</u>	9
	<u>pseudocupidineus</u>	2°
	<u>bari</u>	2°+
	<u>perchlorus</u>	4
	<u>taracuanus</u>	1° ¹
	<u>tumatumari</u>	2
	<u>roraima</u>	4° ²
	total	24

° External only, without dissection

+ Including holotype

¹ Holotype² Holotype and male paratypes

No one looking at figure 1, which shows the main forms of *elevatus* and the parallel forms of *melpomene*, will be surprised at the confusion of the species (the space in the lower right hand corner of the plate could also have been filled with an equivalent form of *melpomene* which is so rare that I was unable to obtain a specimen to photograph); the parallel variation is further summarised in table 1.

The chief differences between *melpomene* and *elevatus* are summarised in table 2 and illustrated in figure 2, in many specimens of *elevatus* the hook on the genital valve can be seen without dissection; the characters used, the male genitalia and the basal markings of the hindwings, appear to be "good" specific characters in the genus *Heliconius*, showing much less variation than the major wing markings, although they do vary between localities and a little between individuals; the range of variation of both characters in *melpomene* and *elevatus* is distinct and shows no overlap. Table 2 is based on the examination of thousands of *H. melpomene*, between fifty and a hundred of *H.e.elevatus*, perhaps two dozen of *H.e.tumatumari*, the five type specimens of the new subspecies, and not more than a dozen of

each of the other subspecies; table 3 shows the numbers of male genitalia examined. It could be argued that the apparent species are no more than genetic polymorphs. The basal markings are not known to be polymorphic in any other *Heliconius*. Polymorphic genitalia are likewise not known in the genus, although not many specimens of each species have been examined; taxonomists usually underestimate the variability of these organs (Ford 1955) despite the finding of Kerkis (1931) that the genital apodemes of a hemipteron have higher coefficients of variation than other parts of the body; a thorough survey of the African butterfly *Papilio dardanus* Brown showed strong variation and even polymorphism in the male genitalia (Turner 1963a). But if it can be established that the basal markings and genital characters are correlated, so that we do not find *melpomene* markings with *elevatus* genitalia or vice versa, then it becomes highly unlikely that the forms are merely polymorphs, as it would be too great a coincidence for two characters "good" in the rest of the genus to become in one species not simply polymorphic, but controlled by the same genetic switch mechanism.

To check on this I selected from the Tring collection 14 males of *H. melpomene* (7 of the *aglaope* pattern and 7 of the *vicinus* pattern) and 8 of *H. elevatus* (5 of the *elevatus* pattern and 3 of the *perchlorus* pattern) all from the upper Amazon basin; the identification being made by means of the basal marks. The genitalia were prepared by Miss Susan May, an assistant in the Museum, and I then sorted them into *melpomene* and *elevatus* types, without knowing which butterfly they belonged to (all preparations were of course numbered). The result was:

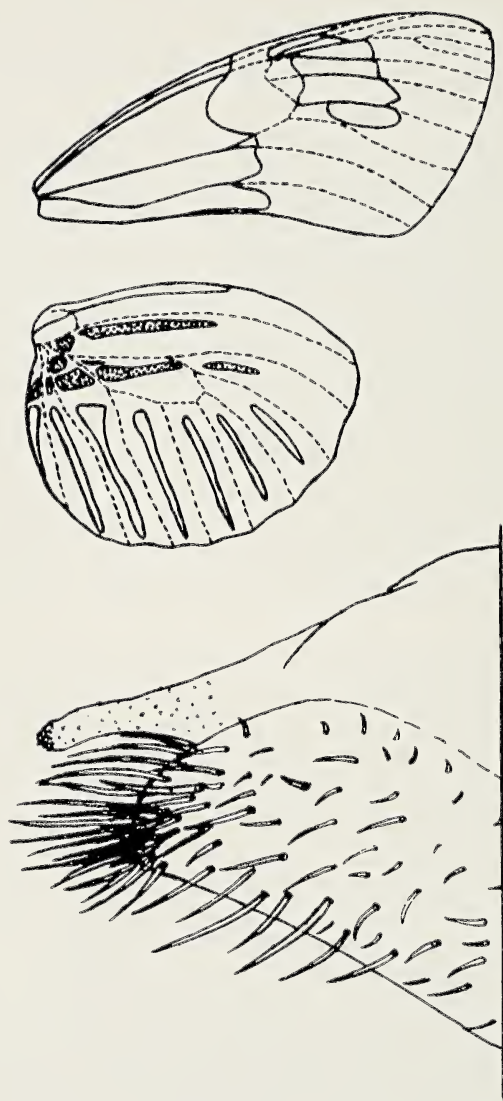
pattern:	<i>elev.</i>	<i>melp.</i>
<i>elev.</i>	7	0
genitalia:		
<i>melp.</i>	3	11

A further *elevatus* had deformed valves. Of the three specimens placed in the "wrong" class, one was simply an error, having ordinary *melpomene* genitalia; the other two had the apical extension longer and more robust than is usual in *melpomene*, but on re-examining them I found that the extensions were still much weaker than those found in *elevatus*. The probability of finding such an association between the wing and genital characters in a sample if there was in fact no association in the total population is less than one in one hundred (Fisher's exact test, two tails).

This is good evidence that *elevatus* is a species distinct from *melpomene*. Recently differences have been found between *H.melpomene* and *H.e.elevatus* in the distribution of the androconia (Emsley 1965).

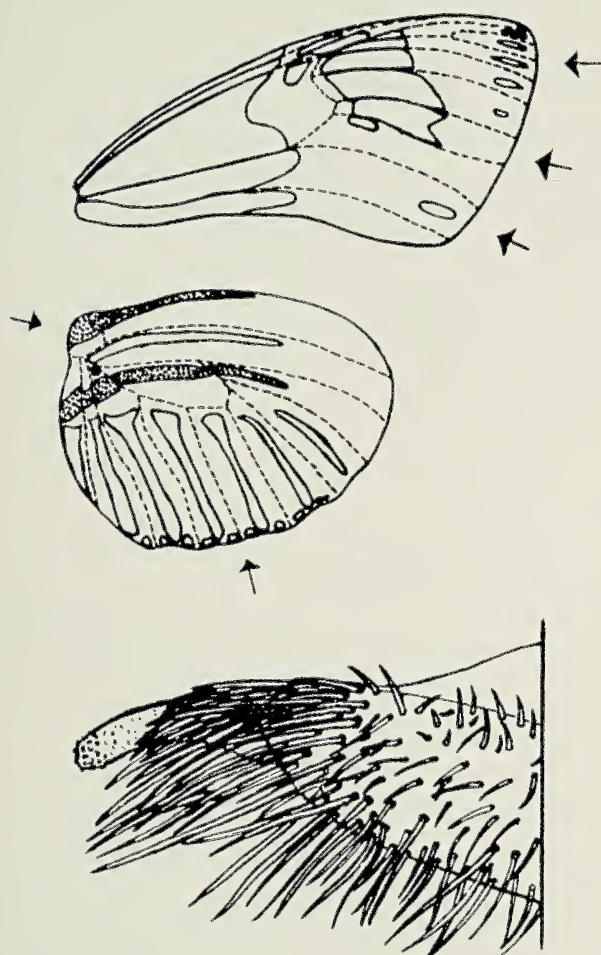
As an aside it is worth considering the possible function of the characters of the male genitalia. Experiments by Lorkovic (1953) have discredited the "lock and key" theory at least for some European butterflies subjected to forced mating (see also other work quoted by Dobzhansky (1951). At least three authors (Lorkovic 1956, Turner 1962, Mayr 1963) are of the opinion that the valves are highly variable within species (and therefore also between species) because natural selection has little effect on their precise shape: if they are gripping organs then it is not of great significance what shape they are, provided that they grip; the ridges in the human "finger print" are analogous. Emsley (1963) claims that on dissecting sundry unnamed Heliconids electrocuted while mating he found that the hooked tips of the genital valves were not touching the female, who was gripped by the median organs (uncus etc.) and possibly by the bases of the valves.

It is very surprising that a hook on the end of a genital valve should be functionless. If the solution to the puzzle is not that the male's muscles had been contracted by the electrocution, then it probably rests in the courtship behaviour of the butterflies; my own unpublished observations of the Heliconid species *Dryadula phaetusa* (Linnaeus), which has large appendages at the tips of the valves, are typical of most Heliconid courtships. When the female settles after the courtship flight, the male alights by her side, facing in the same direction, and by bending his abdomen in a semi-circle grips the tip of the female's abdomen with his genitalia; this done he moves so that his abdomen and that of the female are in direct line, and the butterflies face in opposite directions; they remain in this position until they part. It is possible, and this could be checked by watching matings of males whose genitalia had been clipped, that the hooks at the tips of the valves grip the female during the first phase of copulation when the couple are facing in the same direction, and that on moving his position the male changes his grip on the female, holding her from then on with median organs and the bases of the valves. The small hooks of *H.melpomene* and some other species may be vestigial.



melpomene

Fig. 2. Differences between *H. elevatus* and *melpomene*, as shown by the forewing upperside, hindwing underside, and the tip of the male genital



elevatus

valve. Basal marks on the hindwing are shaded if red, unshaded if yellow; no other marks are shaded.

Appended is a synopsis of the infra-specific forms of *H.elevatus*, followed by a description of a new subspecies. A drawer in the main collection of the British Museum (Natural History) at Tring shows all the subspecies of *H.elevatus*. A distribution map, and a discussion of the interesting taxonomic and mimetic relations of *elevatus* with other *Heliconius*, will appear in a detailed study of the genus now in preparation. *H.elevatus* seems to be closely related to, or perhaps conspecific with *H.luciana* Lichy, a species with a superficially very different pattern resembling that of *H.antiochus* (L.) (see Lichy 1960).

In the following list only the most important references are given; the short description refers to the characters differentiating the subspecies: shape of the yellow band, presence or absence of apicals and presence or absence of hindwing rays (fig. 2).

Subspecific epithets have, where necessary, been given masculine endings in accordance with the *Code*, although I am by no means convinced of the wisdom of this. The subgenus is that of Michener (1942).

Heliconius (Heliconius) elevatus Nöldner

1. *H. elevatus elevatus* Nöldner

Heliconius elevatus. Nöldner, 1901, *Berlin.ent.Zeit.* 46, 5.

Heliconius melpomene elevatus. Stichel & Riffarth, 1905, *Tierreich* 22, 120; Stichel, 1906, *Gen.Ins.* 37,25.

Heliconius elevatus. Eltringham, 1917, *Trans.R.ent.Soc.Lond.* 1916, 134.

Heliconius elevatus elevatus. Neustetter, 1929, *Lep. Cat.* 36, 52.

Heliconius melpomene f. *elevatus*. Emsley, 1964, *Zoologica* 49, 262.

Heliconius elevatus elevatus. Emsley, 1965, *Zoologica* 50, 210. Narrow band; no apicals; hindwing rays. Upper Amazon basin. The form *griseoviridis* (*H.elevatus* f. *griseoviridis* Neustetter, 1938, *Ent. Rundsch.* 55, 416) is a minor variation in which the band is extended posteriorly and proximally by an area of mixed black and yellow scales.

Form *noeldneri* (*H.elevatus* f. *nöldneri* Neustetter, 1938, *Ent. Rundsch.* 55, 415) has abnormally strong development of red marks, having red proximal to the band, a hammer-headed red band extending from the basal red along Cu_2 to the margin of the forewing, two rows of red subapical spots on the forewing, and abnormally wide heads to the rays on the hindwing. It gives the impression of reverting toward the "Tiger" pattern of those *Heliconii* which mimic Ithomiids.

The types of both these varieties, in the Naturhistorisches Mu-

seum, Wien, come from Yurimaguas, Peru; their relation with the following subspecies is not clear.

2. *H.elevatus pseudocupidineus* stat.nov.

Heliconius elevatus f. *pseudocupidineus*. Neustetter, 1931, *Int.ent.Zeit.*, Guben 25, 169.

As *H.e.elevatus*, but band very much narrower. Perhaps only just worthy of subspecific rank. Tarapoto and Yurimaguas, N.E. Peru. Types (one male, one female) in the Naturhistorisches Museum, Wien. I select the male as the lectotype of the new subspecies.

Labels on the lectotype: (1) *elevatus* f. *pseudo*=/*cupidineus* Neust./ ♂ Type. (2) Yurimaguas/Peru/O. Michael. (3) Coll./Neustetter. (4) *H.elevatus pseudocupidineus*,/lectotype (Turner). The form *nigromacula* (*H.elevatus* f. *nigromacula* Neustetter, 1932, *Zeit.österr.Ent.Ver.*, Wien 17, 15) appears to be similar to form *noeldneri* (but with a narrower band). I have not seen the type.

3. *H.elevatus perchlorus* Joicey & Kaye

Heliconius elevatus perchlora. Joicey & Kaye, 1917, *Ann.Mag. nat.Hist.* (8) 20, 94; Neustetter, 1929, *Lep. Cat.* 36, 52.

Heliconius melpomene f. *perchlorus*. Emsley, 1964, *Zoologica* 49, 262.

Heliconius elevatus perchlorus. Emsley, 1965, *Zoologica* 50, 210.

Broad band; no apicals; hindwing rays. Bolivia, valleys north-east of Lago Titicaca. Type in the British Museum (Natural History); no locality data.

4. *H.elevatus taracuanus* Bryk. Comb.nov. et subspecies dubia

H.melpomene taracuanus. Bryk, 1953, *Ark.Zool.* 5(1), 76.

Broad band; no apicals; hindwing rays. Taracua, Rio Uaupés (a tributary of the Rio Negro), state of Amazonas (Brasil). Type in the Naturhistoriska Riksmuseet, Stockholm.

This specimen is undoubtedly an *elevatus*, not a *melpomene*, and is very similar to *perchlorus*; individuals of this phenotype occur among the *e.elevatus* on the upper Amazonas, so it is not clear whether *taracuanus* is simply an intrapopulation variety or whether there are monomorphic populations of this phenotype in the basin of the Rio Negro which grade into the populations on the Amazonas.

5. *H.elevatus bari* (Oberthür). Comb.nov.

Heliconia bari. Oberthür, 1902, *Etudes d'entomologie* 21, 23.

Heliconius melpomene bari. Stichel & Riffarth, 1905, *Tierreich* 22, 120; Stichel, 1906, *Gen.Ins.* 37, 25.

Heliconius melpomene thelxiope forma *aquilina*. Neustetter, 1925, *Zeit.österr.Ent.Ver.*, Wien 10,12. Syn.nov.

Heliconius elevatus schmassmanni. Joicey & Talbot, 1925, *Ann.Mag.nat.Hist.* (9) 16, 647. Syn.nov.

Heliconius melpomene melpomene forma *bari*. Neustetter, 1929, *Lep. Cat.* 36, 51.

Heliconius elevatus aquilina. Neustetter, 1929, *Lep. Cat.* 36, 52.

Heliconius elevatus aquilina forma *schmassmanni*. Neustetter, 1929, *Lep.Cat.* 36, 52.

Heliconius melpomene X *Heliconius aoede*. Emsley, 1965, *Zoologica* 50, 210.

Broken band; apicals present or absent; hindwing rays. Mato Grosso and north Bolivia (*schmassmanni*), Rio Tapajos (state of Pará) and Guianas (*bari*). Types of *bari* and *schmassmanni* in the British Museum (Natural History), the first in the Levick Collection; localities "Guyane française" and "River System, Cuyaba-Corumba, Mato Grosso, Brasil" respectively. Types of *aquilina* (one male, one female) in the Naturhistorisches Museum, Wien; locality "Rio Machados, Mato Grosso." Clearly the male is the lectotype, and I have labelled it as such. The type of *bari* has apical spots, those of *schmassmanni* and of *aquilina* lack them, so one could regard *bari* and *schmassmanni* as separate subspecies, the one in the north and the other in the south, but the difference is small and based upon too few specimens.

6. *H.elevatus tumatumari* Kaye. Comb. et stat. nov.

Heliconius tumatumari. Kaye, 1906, *Entomologist* 39, 53; Eltringham, 1917, *Trans.ent.Soc.Lond.* 1916, 134.

Heliconius melpomene melpomene forma *tumatumari*. Neustetter, 1929, *Lep.Cat.* 36, 44.

Heliconius melpomene X *Heliconius aoede*. Emsley, 1965, *Zoologica* 50, 212.

Broken band; apicals; no hindwing rays. Potaro River, Guyana (=British Guiana).

7. *H.elevatus roraima* subsp.nov.

Heliconius melpomene, form near to *eulalia*. Hall, 1939, *Agric.J.Brit.Guiana* 10, 39; 1940, *Brit.Guiana Dept.Agric. Ent.Bull.* 3, 15.

Heliconius elevatus, form. Emsley, 1965, *Zoologica* 50, 212.

Broad band; no apicals; no hindwing rays. Region of Mount Roraima, Guyana. Types in the British Museum (Natural History). Emsley (1965) reports a long series in the American Museum of Natural History.

Heliconius (Heliconius) elevatus roraima subsp. nov.

Holotype male (fig. 2, E). Upperside: Forewing black-brown, the proximal third extensively marked with red posteriorly from vein Sc to just anterior to the posterior margin; the red being traversed by black-brown along the veins, along a line running longitudinally down the centre of the cell, and a line which runs posterior to vein 1A for 3 mms. from the proximal edge of the wings (venation is after Michener 1942), becoming coincident with the vein distally. At the base of this dark line, a yellow spot. The distal third of the cell, and portions of the wing between Sc, R₁, R₂, M₁, M₂, M₃, Cu₁, Cu₂, and posterior to Cu₃ occupied by yellow areas giving the effect of a large yellow mark invaded by black along the veins. The yellow marks between M₃ and Cu₁ and between Cu₁ and Cu₂ have V-shaped indentations distally.

Hindwing black-brown, a sub-triangular area about 1 cm. long and 2 mms. deep near the base being red, traversed by black-brown veins; posterior to the edge of this red mark three diffuse red markings lying between the veins. Anterior to the red triangle a silver-brown area extending right across the anterior margin of the wing.

Underside: forewing as upperside, except that the black line in the cell is broader, that all the wing posterior to the cell and Cu₁ is silver-brown, without markings, and that there is a basal red mark 5 mms. long between the anterior margin and vein Sc.

Hindwing black-brown, a red line 4 mms. long extending from the base along the anterior margin; 2 mms. posterior to this, and lying just posterior to vein R₁ + Sc a yellow line 10 mms. long. A red line extending across the cell and proximally in a slight curve, following chiefly the position of the posterior edge of the red triangle on the upperside; posterior to this a row of four red marks, the three distal ones occupying the same position as the three red marks on the upperside.

Antennae black-brown, slightly red-brown along one edge. Head black-brown, with white marks above and below the insertion of the antennae and on the ventral side of the palpal segments. Thorax with dorso-lateral yellow markings, but with too many scales missing for a detailed description. Abdomen black-brown, the first segment with two dorso-lateral spots. Genital valves (as seen in hand lens, without dissection) with strong hook at tip.

Labels: (1) Type/HT

(2) Roraima./B. Guiana./H. Whitely.

(3) ♂

(4) Godman-Salvin/ Coll. 1913-2

(5) *Heliconius elevatus/ roraima* Turner 1967/Holotype

Dimensions — forewing: 3.8 cms.; antenna: 2 cms.; body from head to tip of abdomen: 2.6 cms.

Paratype male, labelled as the holotype except that (1) and (5) read "Paratype": similar except that some of the small underside marks on the hindwing are obscure or missing.

Paratype male, labelled (in manuscript ink) Roraima./Bt. Guiana/ (printed) Crowley/Bequest./1901 — 78 and with paratype label as above. Similar to type except for obscurity of some small underside hindwing markings.

Paratype male, labelled (in pencil)? Roraima/ (printed) Crowley/Bequest./1901 — 78 and with paratype labels as above. Similar to the holotype, except that the row of red dots on the upper and underside of the hindwings is absent.

Paratype female, labelled as the holotype, except that (3) is "♀" and (1) and (4) are paratype labels. Differs from the holotype in that the silver-brown areas of both wings are less extensive and less obviously differentiated in colour from the rest of the wing (a characteristic expression of sexual dimorphism in the genus *Heliconius*); the diffuse red marks on the hindwing are missing on the upperside and obscure on the underside; on the forewing the yellow mark posterior to Cu_2 is absent; and the yellow mark between M_3 and Cu_1 has a slightly curved edge instead of the V indentation; and the tips of the antennae are obviously rufous.

Holotype and paratypes in British Museum (Natural History).

The "red" of the above descriptions refers to a pigment which changes colour over the years; it is now an orange red, but was probably a brilliant carmine red when fresh; similarly the "black-brown" was probably almost black.

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SUMMARY

The South American butterfly *Heliconius elevatus* has seven subspecies, all resembling closely various forms of *H. melpomene*; the two species differ in the male genitalia and the detailed marks on the underside of the hindwings. Correlation between the characters of the wings and genitalia show that *elevatus* is a distinct species and not a form of *melpomene*, with which it is usually confused. The nomenclature of *H. elevatus* is summarised, and a new subspecies described.

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COMPARATIVE SPECIATION IN TWO BUTTERFLY FAMILIES, PIERIDAE AND NYMPHALIDAE

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IT IS NOWADAYS GENERALLY ACCEPTED that the main factors influencing evolution are mutation, recombination, selection, chance, and isolation. Naturally these five factors do not play the same rôle in all groups of animals and plants. Thus, for instance, the evolution of polyploid forms is of much greater importance in plants than in animals. Similarly the selective forces affecting the evolution of protozoans and mammals must be very different. The branch of biology dealing with such problems we may call comparative evolution in analogy with comparative anatomy.

Comparative speciation, with which this paper is concerned, is a part of this science. An important method is here to compare the differences existing between the closest related species of different groups. Such differences must be the result of the evolution having taken place since the time of the common ancestral form. It is possible that the differences evolved are an integrating part of the mechanism isolating the two species. In other cases the differences may be the result of adaptations to different environmental conditions or be just a matter of chance.

The two groups discussed here are the two butterfly families *Pieridae* and *Nymphalidae*. All sympatric closely related European species of these two families are compared. To these species the two North American sibling species *Colias eurytheme* and *C. philodice* have been added as they are especially well known predominantly from the investigations by Hovanitz (1943, 1948, 1949 a, b).

Fam. Pieridae.

1. *Pieris napi* L. — *P. bryoniae* Ochs.

These two forms do not behave as different species in all areas where they meet. They do however in some areas which justifies a discussion of their differences.

Male patterns rather similar.

Female patterns more extended in *bryoniae* than in *napi*. Male wing color similar, female wing color white in *napi*, yellow in *bryoniae*.

Genitalia similar (Drosihn 1933).

Foodplants: *napi*: various cruciferous plants.

bryoniae: *Biscutella laevigata*.

2. *Pieris napi* L. — *P. ergane* Hbn.

The patterns of *ergane* are closer to those of *P. rapae* than to those of *napi*. The color of the females is sometimes yellow in *ergane*, less often in *napi*. The genitalia are similar (Drosihn 1933) as well as the scent of the males (Lorkovic, personal communication).

Foodplants: *napi*: various cruciferous plants.

ergane: various cruciferous plants (Forster and Wohlfahrt 1955, Verity 1947), *Aethionema saxatile* in the French Alps and Pyrenees (Descimon 1964, 1966). The very local occurrence of this species makes a wide variety of foodplants rather unlikely.

3. *P. rapae* L. — *P. manni* Mayer.

The patterns of the two species are rather similar, the background color of the females less yellow in *manni* than in *rapae*. Genitalia similar.

Foodplants: *rapae*: various cruciferous plants.

manni: *Diplotaxis tenuifolia* (Italy), *D. erucoides*, *Lepidium graminifolium*, *Iberis* spp., not on cultivated cruciferous plants (Verity 1947).

4. *Colias hecla* Lef. — *C. nastes* Bdv.

The patterns are markedly different in the males, less so in the females. The color is in both sexes orange in *hecla* and yellow in *nastes*.

Genitalia very similar. The number of teeth of the aedeagus on the average slightly higher in *hecla*. Only one specimen of 41 + 34 outside the range of variation of the other (Petersen 1963 b).

Foodplants: *hecla*: *Hedysarum americanum*, *Astragalus alpinus*.

nastes: *Astragalus deflexus* and *alpinus*.

5. *C. hyale* L. — *C. australis* Ver.

Slight differences are present in the patterns. The yellow color in *australis* is more "beautiful", in *hyale* more greenish and "dirty" (Reissinger 1960).

Genitalia slightly different (Warren 1951, Beuret 1951, Bretschneider 1959, Schadewald 1959). Berger and Fontaine (1947), Reissinger (1960), and Petersen (1963 b) found no differences.

Foodplants: *hyale*: various leguminose plants.

australis: *Hippocrepis comosa*.

Male scent: *hyale*: strong aromatic scent (Berger and Fontaine 1947), rather peppery (Riley 1961).

australis: absent or almost absent (Berger and Fontaine 1947), sweetish, honeylike (Riley 1961).

6. *C. myrmidone* Esp. — *C. erate* Esp.

The patterns are markedly different in the males less so in the females. The color is orange in *myrmidone*, usually yellow in *erate*.

Genitalia very similar (Petersen 1963 b).

Foodplants: *myrmidone*: *Cytisus* spp.

erate: unknown.

7. *C. eurytheme* Bdv. — *C. philodice* Gdt.

As in two of the previous *Colias* species the pattern differences are greater in the males than in the females. Color is in *eurytheme* orange, in *philodice* yellow.

Genitalia very similar (Petersen 1963 b).

Foodplants: *eurytheme*: *Medicago*.

philodice: *Trifolium*.

Male scent of *eurytheme* like sweet heliotrope.

8. *C. aurorina* H. Sch. — *C. sagartia* Led.

Pattern differences about the same as in previous species. The color is in *aurorina* orange, in *sagartia* bluish green.

Genitalia very similar (Petersen 1963 b).

Foodplants unknown.

Only *C. aurorina* occurs in Europe. *C. sagartia* lives in S. W. Asia.

9. *Gonepteryx rhamni* L. — *G. cleopatra* L.

There are hardly any patterns on the wings of the two species. The forewings of *cleopatra* males are orange except along the borders, and the yellow color is more saturated. The females of *cleopatra* have yellow borders on the wings.

Genitalia: uncus much smaller in *cleopatra*, otherwise rather similar (Verity 1947).

Foodplants: *rhamni*: *Rhamnus* spp., *Vaccinium*, *Rosa*, *Prunus spinosa*.

cleopatra: mainly on other *Rhamnus* spp. than

rhamni (Verity 1947).

Male scent: *rhamni*: absent.

cleopatra: rich and powerful, freesia (strong)
(Ford 1945).

10. *Anthocaris cardamines* L. — *A. damone* Boisd. and *A. euphenoides* Stgr.

The two latter species are allopatric but not contiguous. The areas of distribution come fairly close together in Italy (cf. Verity 1947). Their great similarity suggests conspecificity. At least, they may both have arisen jointly from the *cardamines* stock and therefore cannot be treated here as two independent cases.

The differences in pattern between *cardamines* and *damone* are slight compared with the geographical variations within the species. The ground colors of the males (yellow in *damone* and white in *cardamines*) are strikingly different. The differences between the females are slight or none.

Genitalia differences are only of a quantitative nature (Verity 1947).

Foodplants. *cardamines*: various cruciferous plants. *Reseda*.

damone: *Isatis tinctoria* and *canescens*.

euphenoides: *Biscutella* spp.

Fam. Nymphalidae.

Mellicta Billb.

Higgins (1955) divides this genus into twelve species, seven of which occur in Europe. Three of these species, *aurelia* Nick. *deione* Geyer, and *asteria* Freyer together with the subsp. *athalia celadussa* Fruhst. do not redevelop subuncal processes below the tegumen. Verity (1950) is of the opinion that *M. deione* and *athalia celadussa* are most similar and he connects on the other hand *M. aurelia* with *M. asteria*. It may very well be that one subspecies (A_1) of one species is closest to one of the other species (B), while another subspecies (A_2) is closer to a third species (C). *M. athalia* with its marked intraspecific variation in the genitalia may very well be a species of type A. This, however, is of lesser significance in the present investigation as the differences in the genitalia between the forms mentioned are in all cases small but well distinct, colors similar, patterns similar or rather similar.

11. *M. deione* — *M. athalia celadussa*

Colors and patterns similar but variable.

Genitalia: small but distinct differences (Verity 1950).

Foodplants. *deione*: *Linaria* spp., *Antirrhinum* spp.

athalia celadussa: *Melampyrum*, *Plantago*.

12. *M. aurelia* — *M. asteria*.

Colors and patterns similar. *M. asteria* much smaller.

Genitalia. small but distinct differences (Verity 1950 p. 196).

Foodplants: *aurelia*: *Melampyrum*, *Veronica*, *Digitalis*, *Chrysanthemum*, *Plantago*.

asteria: unknown.

13. *Euphydryas cynthia* Schiff. — *E. intermedia* Mén.

Color similar in the females, different in the males. Patterns more different in the males than in the females.

Genitalia: slightly different (Higgins 1950).

Foodplants. *cynthia*: *Alchemilla*, *Plantago alpina* and *lanceolata*, *Viola*, *Vaccinium myrtillus*, *Pedicularis*.

intermedia: *Fraxinus*, *Populus*, *Salix*, *Alnus*, *Viburnum*, *Melampyrum*, *Veronica*, *Scabiosa*, *Plantago*, *Viola*, *Prunus*, *Lonicera* (Verity 1950).

14. *Fabriciana adippe* Rott. — *F. niobe* L.

Color and patterns rather similar on the upper side; on the under side the colors are rather different.

Genitalia: various parts shorter and thicker in *niobe* (Verity 1950).

Foodplants: *adippe*: *Viola* spp.

niobe: *Viola* spp., *Plantago* spp.

15. *Brenthis ino* Rott. — *B. daphne* Schiff.

Patterns are slightly different in both sexes on both sides of the wings. Colors are similar.

Genitalia: Verity (1950 p. 259) states that the differences found by Warren (1944) and dos Passos and Grey (1945) are individual variations present in both species.

Foodplants: *ino*: *Sanguisorba*, *Spiraea*, *Rubus*.

daphne: *Rubus*, *Viola*.

16. *Boloria pales* Schiff. — *B. alethea* Hemming (*arsilache*) Esp.)

Colors are similar in both sexes, patterns slightly different.

Genitalia: I was not able to confirm the differences found by Warren (1944).

Foodplants: *pales*: *Viola* spp.

alethea: *Vaccinium oxycoccus*, *Polygonum* spp., *Viola* spp.

17. *Boloria frigga* Thnbg. — *B. improba* Btl.

B. improba is much darker and smaller than *frigga*. The patterns on the under side are rather similar.

Genitalia: Slight differences are present (Bruun and von Schantz 1949).

Foodplants: *frigga*: *Rubus chamaemorus* (Lingonblad 1946).
improba: probably *Salix herbacea* (Bruun and von Schantz 1949).

In tables 1 and 2 the differences between the species have been summarized and indicated by value symbols. It is not always easy to decide which symbol should be used but the tendency is quite obvious: the differences in patterns are of the same magnitude in both families while differences in color are more marked in the *Pieridae*. Specific differentiation without any or with very little change in the genitalia is the rule in the genera *Pieris* and *Colias*, but has probably also taken place in *Brenthis* and *Boloria*.

When the colors of the *Nymphalidae* are different the differences are usually restricted to the under side, except for intrusion of melanistic scales on the upper side as in *Boloria improba* as compared with *frigga*. In the *Pieridae* the color differences are most striking on the upper side and are due to the intrusion of white, yellow, and orange pterins. In the *Colias aurorina*-group blue pigments are also present. In the genus *Colias* both sexes are different in color, in *Pieris* only the females, and in *Gonepteryx* and *Anthocaris* mainly the males. In the genera *Pieris* and *Colias* where the interspecific variation in female color is greatest, the differentiation in the male genitalia is less pronounced.

There are several reasons why closely related pierid species should be more divergent in color than *Nymphalids*. Pterins of white, yellow, and orange color are chemically related. The yellow color of *P. bryoniae flavescens* turns white when the pupae are exposed to pure oxygen during their development. Species of other families do not change color after similar treatment (Deschka and Reichl 1964). A mutation changing the wing color may happen more often in butterflies having pterins in their wing scales than in other Lepidoptera.

The colors of butterflies have several functions: warning, concealment, sexual attraction and stimulation. In connection with isolation between species the sexual functions are of special interest. The colors of the females are known to attract the males though supraoptimal colors sometimes are present (Tinbergen et al. 1952, Petersen et al. 1952). Thus the yellow color

of *P. bryoniae* females is less attractive to their males than the white color (without ultraviolet) of *napi* females and males of both forms. Yellow color may have a higher selective value because yellow females are less likely to hybridize. The yellow color may also be part of a protective coloration.

The colors of the males have been supposed by Ford (1953, 1965) to have a sexually stimulating effect. As far as I know conclusive experiments are still lacking. The presence of strikingly different colors in so many sibling species supports Ford's hypothesis and makes experimental evidence even more desirable.

Differences in the foodplants of the larvae are very marked. In one case only, *P. napi* - *ergane* some authors mention "different cruciferous plants" for both species. *Aetionema saxatile* is at least in France the most important foodplant for *ergane*.

In nine of the seventeen pairs of table 1 one of the species has a very wide distribution compared with the other. These species have been underlined in the table. As *P. napi* is present in two pairs there are together eight species of this kind. These eight species are all adapted to a temperate climate, some of them also to colder and warmer climates. Their larvae live in seven cases on plants of more than one genus while six of the species with restricted distributions live on only one plant genus, usually on a single species. Ecologically they are adapted to an Arctic or alpine climate or to the climate of the Mediterranean area.

The wider ecological amplitude of the central species compared with the 'edge' species is in agreement with the ideas of Brown (1957). He points out that central species are more "potent" and therefore the source of higher categories. Contrary to this Mayr (1954) has stressed the importance of the edge populations, especially on islands. Such isolated populations can under unique environmental conditions form the real novelties of the animal world. It may be noted that the only novelty (not *real* novelty) among the species treated here belongs to the edge species: *Boloria improba*. Living at a higher altitude than any other Scandinavian butterfly and with a concealing coloration well adapted to the dark rocks and stones at this it may be potentially equivalent to the many small *Erebia* and *Mellicta* spp. etc. of the higher parts of the Alps. However, the evolution of a new (sub) genus under such extremes is rendered less

Species	Differences in				Larval foodplant
	pattern	color	genitalia		
family Pieridae	♂	♀	♂	♀	
1. <u>PIERIS NAPI</u> / <u>bryoniae</u> (a)	(+)	-	+	-	cruciferous plants / <u>Biscutella laevigata</u>
2. <u>PIERIS NAPI</u> / <u>ergane</u> (m)	(+)	-	(+)	-	cruciferous plants / <u>cruciferous plants</u> <u>Aethionema saxatile</u>
3. <u>P. RAPAE</u> / <u>manni</u> (m)	(+)	-	(+)	-	cruciferous plants / <u>Diplotaxis tenuifolia</u>
4. <u>Colias hecla</u> (a) / <u>C. nastes</u> (a)	+	(+)	+	-	<u>Hedysarum americanum</u> , <u>Astragalus alpinus</u> / <u>Astragalus deflexus</u> , <u>alpinus</u>
5. <u>C. HYALE</u> / <u>australis</u> (m)	(+)	(+)	(+)	- ?	leguminous plants / <u>Hippocrepis comosa</u>
6. <u>C. myrmidone</u> / <u>erate</u>	+	(+)	+	-	<u>Cytisus</u> spp. / unknown
7. <u>C. erytheme</u> / <u>philodice</u>	+	(+)	+	-	<u>Medicago</u> / <u>Trifolium</u>
8. <u>C. aurorina</u> / <u>sagartia</u>	+	(+)	+	-	unknown
9. <u>Goneperyx rhamni</u> / <u>cleopatra</u> (m)		+	+	+	<u>Rhamnus</u> spp., <u>Vaccinium</u> , <u>Rosa</u> / <u>Rhamnus</u> spp.
10. <u>Anthocharis cardamines</u> / <u>damone</u> + <u>euphenoides</u> (m)	(+)	+	(+)	+	cruciferous plants / <u>Isatis tinctoria</u> + <u>Biscutella</u> spp.
family Nymphalidae					
11. <u>MELICTA ATHALIA celadussa</u> (+) / <u>deione</u> (m)	(+)	-	-	+	<u>Melampyrum</u> , <u>Plantago</u> / <u>Linaria</u> <u>Antirrhinum</u>
12. <u>M. aurelia</u> / <u>asteria</u> (a)	-	-	-	+	<u>Melampyrum</u> , <u>Plantago</u> , <u>Veronica</u> <u>Digitalis</u> , <u>Chrysanthemum</u> / unknown
13. <u>Euphydryas Cynthia</u> (a) / <u>intermedia</u> (a)	+	(+)	+	+	<u>Achemilla</u> , <u>Plantago</u> , <u>Viola</u> , <u>Vaccinium</u> , <u>Pedicularis</u> / <u>Fraxinus</u> , <u>Populus</u> , <u>Salix</u> , <u>Plantago</u> , <u>Viola</u> , <u>Alnus</u> , <u>Viburnum</u> , etc.
14. <u>Fabriciana adippe</u> / <u>niobe</u>	(+)	+	+	+	<u>Viola</u> / <u>Viola</u> , <u>Plantago</u>
15. <u>BRENTIS INO</u> / <u>daphne</u> (m)	(+)	-	-	+	<u>Sanguisorba</u> , <u>Spiraea</u> , <u>Rubus</u> , / <u>Rubus</u> , <u>Violaceae</u>
16. <u>Boloria alethea</u> / <u>pales</u> (a)	(+)	+	-	- ?	<u>Viola</u> , <u>Vaccinium</u> <u>occycoccus</u> , <u>Polygonum</u> , / <u>Viola</u>
17. <u>Boloria frigga</u> / <u>improba</u> (a)	+	+	(+)	+	<u>Rubus chamaemorus</u> / <u>Salix herbacea</u>

Table 1. Presence or absence of differences in some characters between sibling species of the families Pieridae and Nymphalidae. (+) = slight differences in color and pattern. Species in caps = widely distributed species. a = adapted to arctic or alpine climate; m = distribution mainly in the Mediterranean area.

probable on account of the hazardous conditions for survival during the long time required for such a process.

The more restricted ecological amplitude of the edge species may in some cases depend on competition from the central species. Sometimes, however, this is certainly not the explanation. *P. bryoniae* and *A. euphenoides*, two edge species, both live on *Biscutella*. This is the only plant genus of the family *Cruciferae* which is common at the altitude where the butterflies live. The close relationship larva — foodplant might from the beginning have been more or less a matter of coincidence following the adaptation to a certain climate and a plant family as source of food.

However, as soon as the relationships have become established they become closer. When today *P. bryoniae* lives on *Biscutella* on the southern side of the Alps it is able to compete with *P. napi* down below 300 m (Posavje, near Ljubljana, Yugoslavia). When both live on *Arabis halleri*, as on Monte Mottarone in the Italian Alps, the lower limit of *bryoniae* is at 700 m (Petersen 1955).

By their morphology the edge species are exposed to a different selection than the central species. The polyphagy of the central species leads to an increase of the variation of their populations. The greater variation of the central species by the combination of geographic variation and dispersal (Mayr 1954) is in this way increased.

		patterns			color			genitalia			larval foodplant	
		+	(+)	-	+	(+)	-	+	±?	-	Over- lapping	different
<u>Pieridae</u>	♂	4	5	0	6	1	3	2	1	7		
	♀	1	8	0	5	5	0				3(2)	5(6)
	total	5	13	0	11	6	3	2	1	7		
<u>Nymphalidae</u>	♂	2	4	1	2	1	4	5	2	0		
	♀	1	5	1	1	1	5				4	3
	total	3	9	2	3	2	9	5	2	0		

Table 2. Differences between sibling species of the families Pieridae and Nymphalidae according to table 1.

ISOLATING MECHANISMS

Ethological isolation. The differences between species leading to ethological isolation are thus different in the two families investigated. Pieridae often have different colors and in at least two cases different scents (*G. hyale-australis* and *G. rhamnicleopatra*). Two species have separated from *P. napi* without developing recognizable scent differences.

The attractiveness of the color in *P. napi* is reduced to about 1/10 by a very small amount of yellow pterins in the wings (Petersen 1963 a p. 224). Bees in training experiments are able to separate four colors only (Hertz 1937). Perhaps the reaction of the *napi* butterflies means that a limit between two of the colors in their color vision is situated between white (without ultraviolet) and the same white with a slight mixture of yellow.

A similar slight difference is present in other pairs (*napi - ergane*, *rapae - manni*, and *cardamines - euphenoides*). It is possible that a + from the point of view of the butterflies is a better expression of the differences than the (+) of table 1.

The genitalia of many species of insects and other animals are often so characteristic that they enable the separation of closely related species (cf. Dobzhansky 1941 p. 267). This has given rise to the lock-key theory. According to this theory the genitalia of males and females of a species match another so exactly that even a small deviation makes copulation physiologically impossible. Some experiments and observations tend to support to the lock-key theory but others show that the original formulation was strongly exaggerated. Even after the removal of large parts of the genitalia except the aedeagus a male is able to copulate with a female of its own species (Sengün 1944, Lorkovic 1953). These results led to the conclusion that a structural change played no rôle in the isolation between species. No quantitative estimation of the isolation (e. g. by choice experiments) has ever been made. Observations by Standfuss (1896), Federley (1932), and Sturtevant (1921) show that different genitalia probably cause a certain isolation.

Differences between related species are more common where the genitalia have complicated structures as in the *Nymphalidae*. In groups with less complicated genital apparatus (as in fam. pieridae) inter- and intraspecific variation is smaller. Dobzhansky, (l. c.) suggests that a complicated structure is more often changed in connection with the genetic revolution within a population. However, this does not explain the evolution of the

complicated structures which in many groups are more common in the genitalia than in any other part of the body. This may be explained by a greater efficiency of a complicated genital apparatus. The possibility of a greater chance of developing isolation between species as a factor promoting complication of structure cannot be excluded. A character which permits rapid speciation (within reasonable limits) must in the long run have a positive selective value.

The ecological isolation is to a great extent dependent on the larval foodplant. The "typical" condition with a central species of wide distribution and a wide variety of foodplants and an edge species living on a single plant genus or species is present in only four (five) pairs (1, 3, 5, 10, perhaps also in 2), all of the family Pieridae. In another four pairs the foodplants are different, in seven (six) partly overlapping. No species have the same foodplants.

In four pairs one of the members is a lowland species, the other a mountain species. As a consequence of this difference not only a spatial but also a temporal isolation exists as the mountain species are on the wing later in the season.

Hybrids between sibling species have been found in several cases, though only within the family Pieridae. The hybrids between *C. eurytheme* and *philodice* show good though slightly lowered vitality (Hovanitz 1953). A similar result was obtained by Petersen and Tenow (1954) in crosses between sympatric *bryoniae* and *napi* from the northern Alps. In both cases the vitality of F₂-specimens was low. F₂-specimens of normal vitality were obtained by Bowden (1956) when crossing *P. bryoniae* from the Alps with English *napi*.

In the genus *Colias* a number of different hybrids have been found, for instance *sagartia* x *aurorina* (Lederer 1941) and *nastes* x *hecla* (Hovanitz 1963) among the pairs studied. Hovanitz (l. c.) mentions another seven combinations of *Colias* hybrids described in the literature.

In the genera *Pieris* and *Anthocaris* extensive hybridization experiments have been made by Lorkovic (1928, 1953). In crosses *P. manni* ♀ x *rapae* ♂ only males were obtained, a characteristic not uncommon among Lepidoptera. The reciprocal cross is in this respect normal. All hybrids are sterile. The ovaries of the females are rudimentary.

Hybrids were obtained in the following crosses too, though the sexes are not mentioned.

<i>P. napi</i> ♂	x	<i>ergane</i> ♀
<i>P. napi</i> ♂	x	<i>manni</i> ♀
<i>P. napi</i> ♂	x	<i>rapae</i> ♀
<i>A. cardamines</i> ♂	x	<i>euphenoides</i> ♀
<i>A. cardamines</i> ♂	x	<i>ausonia</i> ♀

Adult F_1 hybrids are thus obtained even between species less closely related than those counted as sibling species here. It seems, however, doubtful whether any of these hybrids exist in nature.

The fact that so many more hybrids of *Pieridae* than of *Nymphalidae* have been found in nature can be explained in several ways:

1. The *Pieridae* have in this respect been much more closely studied.
2. Hybrids are more easily detected in the *Pieridae* because of the clearcut difference in color and pattern.
3. Sibling species in the *Pieridae* are genetically more similar because genetically similar populations can become isolated ethologically by color differences.

Of the two families *Pieridae* and *Nymphalidae* the latter is the most successful in so far as it has a higher number of species. The only factor among those investigated which could be responsible for this is the more complicated structure of the genitalia. Only the investigation of a greater number of families could give the answer whether this is an important factor in the evolution of species.

SUMMARY

Ten pairs of sibling species, mainly European, of the family *Pieridae* and seven of the family *Nymphalidae* are compared. Differences in patterns, color, male genitalia, larval foodplants, and distribution have been investigated.

The *Pieridae* are more often different in color, the *Nymphalidae* in the male genitalia. The differences are of about the same size in the patterns of both families.

The differences in color between *Pierids* are attributed to the greater chance in this family of a mutation markedly changing the color due to the presence in the wings of chemically related pterins of white, yellow, and orange color. These colors are supposed to be sexual attractants and stimulants as has been proved for the white color of *P. napi*.

The greater differences in the genitalia between *Nymphalid*

species are connected with more complicated structures in this family.

The foodplants of the larvae are markedly different in 8 of the 15 pairs where they are known.

Species with a wide range usually live on a greater number of foodplants.

In almost all pairs one of the species lives in the Mediterranean area or is adapted to Arctic or alpine conditions. Only under such circumstances geographical isolation leading to speciation was possible.

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THE BUTTERFLY FAUNA OF A YELLOW PINE FOREST COMMUNITY IN THE SIERRA NEVADA, CALIFORNIA

OAKLEY SHIELDS

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Below is a list of butterflies I collected in the vicinity of Carnegie Experimental Garden, 4600 feet, one mile east of Mather, Sierra Nevada Mountains, Tuolumne County, California. These were collected in an area of about one square mile during three summers: June 19 to September 6, 1964; June 14 to August 9, 1965; and June 20 to September 9, 1966.

The area is a Transition Zone with a Yellow Pine Forest plant community; *Pinus ponderosa*, *Libocedrus decurrens*, and *Quercus Kelloggii* are the predominant trees. Other indicator plants present are *Abies concolor*, *Ribes Roezlii*, and *Ceanothus integerrimus*. This plant community can be subdivided into micro-habitats of wet and dry meadows, stream banks, forest glades, and open and tree covered benches and slopes.

PAPILIONIDAE

Papilio zelicaon
Papilio rutulus
Papilio multicaudata
Papilio eurymedon

PIERIDAE

Neophasia menapia
Pieris protodice
Pieris rapae
Colias eurytheme
Anthocaris lanceolata
Euchloe creusa hyantis

DANAIDAE

Danaus plexippus

SATYRIDAE

Coenonympha tullia
californica

Cercyonis silvestris

NYMPHALIDAE

Limenitis lorquini
Adelpha bredowii
californica
Vanessa atalanta
Vanessa virginiensis
Vanessa cardui
Vanessa carye
Junonia coenia
Nymphalis californica
Nymphalis antiopa

Polygonia faunus rusticus

Chlosyne palla

Phyciodes mylitta

Phyciodes campestris

Euphydryas chalcedona

Euphydryas editha rubicunda

**Speyeria zerene*

Speyeria callippe inornata

**Speyeria hydaspe*

Speyeria mormonia arge

**Speyeria cybele leto*

LYCAENIDAE

Habrodais grunus

Atlides halesus

Mitoura spinetorum

**Mitoura johnsoni*

**Mitoura nelsoni*

Incisalia augustinus iroides

Incisalia eryphon

Strymon melinus

Satyrium californica

Satyrium saepium

Callophrys dumetorum

Lycaena arota

Lycaena xanthoides

Lycaena editha

Lycaena helloides

Leptotes marina

Plebejus saepiolus

Plebejus icarioides

Plebejus acmon

**Evres amyntula*

Philotes battoides intermedia

Philotes enoptes

Scolitantides piasus

Glaucopsyche lygdamus behrii

Celastrina argiolus echo

HESPERIIDAE

**Amblyscirtes vialis*

Ochlodes sylvanoides

Atalopedes campestris

Polites sabuleti tecumseh

Polites sonora

**Hesperia harpalus yosemite*

Hesperia juba

Heliopetes ericetorum

Pyrgus ruralis

Pyrgus communis

Erynnis persius

Erynnis lucilius afrantius

Erynnis propertius

Thorybes pylades

**Thorybes diversus*

Epargyreus clarus

The species that Garth and Tilden (1963) consider restricted to the Transition Zone in Yosemite National Park are starred (*); only *Colias occidentalis chrysomelas* was not seen at Mather of their 10 species listed as indicators. 12 of 21 species they consider indicative of the Upper Sonoran Zone are also present at Mather. This may be partly explained by the fact that the Upper Sonoran Zone is about one air mile to the north so that some inflow of species might be expected. Also, some of these species breed in the Transition Zone as well, notably *Incisalia augustinus iroides*, *Lycaena arota*, *Thorybes pylades*, and *Epargyreus clarus*.

All of the 33 species listed by Garth and Tilden (1963) as occurring at Mather were duplicated in this study except *Speyeria egleis*. They do not list *Speyeria mormonia arge* for Mather, which is abundant in July in the meadows. The *arge* may have been mistaken for *egleis* since the two closely resemble each other.

Some species were conspicuous by their absence at Mather: *Parnassius clodius sol*, *Polygonia zephyrus*, and *Satyrium sylvinus*. The food plants for all three were abundant. Earlier collecting in the year may produce such species as *Anthocaris sara* and *Incisalia fotis windi*.

Emmel and Emmel (1963) found 74 species in a six square mile area at Donner Pass, Placer County, California, between 6900 and 8300 feet. The zones included Transition, Canadian, and Hudsonian. It is interesting that 48 species (64.9%) are found both at Donner Pass and at Mather, and that the family composition of both places is so similar:

FAMILY	NO. OF SPECIES		% OF TOTAL SPECIES	
	M*	D*	M	D
PAPILIONIDAE	4	5	5.4	6.8
PIERIDAE	6	8	8.1	10.8
DANAIDAE	1	1	1.4	1.4
SATYRIDAE	2	2	2.7	2.7
NYMPHALIDAE	20	20	27.0	27.0
LYCAENIDAE	25	28	33.8	37.8
HESPERIIDAE	16	10	21.6	13.5
totals	74	74	100.0%	100.0%

(*M = Mather, D = Donner Pass)

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IN THIS ISSUE

Morphology of the Immature Stages of *Everes Comyntas*
Godart

Donald A. Lawrence and John C. Downey 61

A Little-Recognised Species of *Heliconius Butterfly*

John R. G. Turner 97

Comparative Speciation In Two Butterfly Families,
Pieridae and Nymphalidae

Björn Petersen 113

The Butterfly Fauna of a Yellow Pine Forest Community

Oakley Shields 127

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OF RESEARCH
ON THE LEPIDOPTERA



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THE PURPOSE OF THE JOURNAL is to combine in one source the work in this field for the aid of students of this group of insects in a way not at present available. THE JOURNAL will attempt to publish primarily only critical and complete papers of an analytical nature, though there will be a limited section devoted to shorter papers and notes. QUALITY WORK on any aspects of research on the Lepidoptera is invited. Analytical and well illustrated works are preferred, with a minimum of long description.

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LABORATORY TECHNIQUES FOR MAINTAINING CULTURES OF THE MONARCH BUTTERFLY.

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and Dept. of Biological Sciences, University of Delaware*

INTRODUCTION

THE METHODS DESCRIBED HERE represent the experiences of many years of work carried on at the University of Toronto and University of Delaware. Some of the procedures reported have been developed at both laboratories while others were developed at one particular laboratory.

Our research has sometimes required mass rearing for migration studies, and at other times the rearing of smaller numbers for studies on various research projects such as the study of scent receptors, scent organs, development rates, virus infections, light periodicity, behaviour, and chemoreceptor stimulation by the food plant.

For student laboratory exercises, the Monarch butterfly has proved to be an effective species for illustrating various aspects of invertebrate physiology such as, location of scent receptors, responses to light and temperature, effects of temperature on development rate, flight mechanisms, and receptor-oviposition responses. The Delaware Laboratory has supplied approximately one hundred Elementary School Teachers in many States with viable eggs with which to carry out studies of the Monarch butterfly life cycle.

The present paper outlines the culturing procedures we have followed in one or both laboratories, with a brief discussion of the use of artificial diets in maintaining living specimens of all stages during the winter months.

ADULTS

Flight Cages (60 cm. x 90 cm. x 90 cm.):

These cages, of wood frame and cloth screen construction, have one side left open. The open end is fitted with a hinged, screened door or is covered with cheese cloth; the latter is preferred since it allows easy access to the interior of the cage without liberating any of the actively flying butterflies, because the

cheese cloth can be pulled slightly aside allowing the specimen to be captured, at the same time keeping the cloth secured both on the cage and around one's arm as one reaches into the cage. This open end also allows for introducing milkweed plants. By turning the cage so that the open end faces upward, it can also be used for mass rearing (Urquhart, 1960).

Oviposition Cage (30 cm. x 30 cm. x 60 cm.):

This is a smaller cage of the same construction as the flight cage, but it is open at the top and bottom. The cage is placed over a growing milkweed plant and the top covered with a piece of glass or a wood frame covered with plastic sheeting or cloth screen. The removable frame top or glass is pushed to one end thus allowing for removal of the eggs from the milkweed plants without allowing the escape of the occupants. The smaller cage forces the gravid females to come into frequent contact with the milkweed plants, thus stimulating more rapid oviposition.

Cylindrical Cage (90 cm. in height x 50 cm. in diam.):

This type of cage is constructed of wire mesh and equipped with two openings — one near the top and one near the bottom. The openings are closed with wire mesh doors which swing open in or out on rings located at the tops of the doors. No latches are required. A wire mesh bottom keeps the butterflies from coming in contact with the honey solution that may have accumulated on the floor of the cage. With the bottom left open, a smaller form of this cage could be placed over a milkweed plant for oviposition.

Cartons and Envelopes:

We have held adults alive for periods in excess of five months in small cardboard cartons (pint-sized freezer cartons). A small cotton pad, soaked in a four per cent honey solution, placed in the bottom of the carton, maintains a high R.H. and, at the same time, supplies the necessary nourishment. The carton is completely sealed. The specimens are held at 7°C. and removed to 21°C. for two hours once each week which allows sufficient activity for feeding and body movement. Specimens were also held in freezer cartons at 16°C. continuously for four months, the temperature being low enough to decrease activity and still sufficiently high to allow for feeding and body movement. The low temperature decreased the incidence of mould formation and decreased the rate of fermentation of the honey solution — the latter was renewed once a week.

Specimens were held in cellophane envelopes (6 cm. x 12 cm.) for periods in excess of one month. A small piece of cotton,

soaked in honey solution, was placed in one corner of the envelope and the butterfly, with wings folded together, was placed in the envelope with its head close to the cotton. The cotton was charged periodically by inserting the needle of a hypodermic syringe through the envelope and into the cotton. The envelope was sealed off by folding the free end and securing it with a paper clip. Specimens were held at 16°C.

Feeding:

Monarch butterflies may be held throughout the winter on a diet of 10% honey-water solution. Among many dispensing methods, the following has proved practical for use with cylindrical cage. Aluminum sheeting 1 mm. thick with 1 mm. holes spaced 1 mm. apart, is bent to fit the outside of the cage and held in place with hooks. The holes in the metal membrane serve as reservoirs for the honey solution. To feed the butterflies, the metal membrane is washed thoroughly and replaced on the cage with the water remaining in the small perforations. It is sometimes necessary to place the specimens in the vicinity of the metal membrane in order to instigate feeding. In doing so, care must be exercised in removing the butterflies from their hold on the cage wire as their tarsi may be broken, making it impossible for them to cling to the cage or to the milkweed plants.

When the butterflies have had a drink of water, honey solution is added to the membrane with a squeeze bottle. It may be necessary to "train" some of the butterflies to use the feeding membrane by first inducing feeding by unrolling the proboscis with the point of a pipette or squeeze bottle and giving the butterfly a small drop of honey solution. They can then be placed on the feeding membrane where they will continue to feed by themselves.

Cheese cloth wicks, suspended inside the cages from one side of the cage to the other, and with the free ends secured by clip pins to the top of the cage, will hold the solution for a twenty-four hour period or more, depending upon the humidity of the environment. Such wicks can be charged with honey solution by means of a squeeze bottle, applying the solution to the free ends of the wick.

Synthetic sponges, cut into thin strips, can be inserted into longitudinal slits (placed near the top of the cage) made in the cloth screen. These can be recharged without opening the cage.

Continuous feeders, designed after the principle of the intravenous feeder, were found useful when the cages could not be

attended to for a few days. This dispenser consists of a gallon jar fitted with a two-holed rubber stopper into which is inserted a glass tube of sufficient length to reach the air space above the liquid when the jar is inverted, and a second glass tube, 10cm. longer than the stopper, protruding a sufficient length to allow for the attachment of a plastic tube approximately two feet long. The jar containing the honey solution, is suspended above the cage in an inverted position. The rate of flow of the solution is controlled by a Hoffman Clamp (screw compressor type). The free end of the wick, suspended from the roof of the cage, passes into a gallon jar.

Plastic vials have been used successfully by G. Grisdale of the Insect Pathology Research Institute, Sault Ste. Marie, Ontario. Shell vials (13 x 35mm) filled with honey solution, are taped together in bundles of six or more. These vial clusters are then suspended from the upper part of the cage.

Humidity:

Humidity is an important physical factor in the successful maintenance of adult butterflies over long periods of time. At the University of Toronto laboratory an R.H. in excess of 90% is maintained in the growth chambers. Adults, collected or reared in late August, have been kept alive until the following April at which time they were successfully mated with resulting viable eggs.

Reproductive colonies are maintained the year round at the University of Delaware in a small laboratory with no special arrangements except the operation of a small humidifier and the maintenance of a temperature between 21° and 27°C. Adults have been kept alive for periods of four months under these conditions.

Oviposition:

Gravid females will readily oviposit on milkweed leaves either as growing plants or as individual leaves suspended in the cage. The plants are placed at the side of the cage that faces the most intense illumination. The butterflies congregate at the side of the cage where the light is most intense thus coming into more frequent contact with the milkweed plants. Scent receptors are located on the mesothoracic legs, (Urquhart, 1960) and contact with the milkweed leaves triggers off the process of oviposition. So long as the tarsi rest upon the leaf, the egg is deposited on any adjacent surface. Thus, eggs may be deposited on a piece of paper placed at the tip of the abdomen. This procedure is especially useful when the eggs are to be shipped

by mail. The eggs develop normally on paper.

Females will oviposit on thawed milkweed as well as on a paste of dehydrated milkweed. Females will sometimes oviposit on a cloth soaked in fermented honey solution. It is not unusual to find hundreds of eggs on the feeder wicks as a result of this peculiar reaction.

Females will lay eggs even when held by the wings. Several eggs may be deposited in quick succession followed by a pause. If the specimen is allowed a brief period of flight, or to move its wings while being held, oviposition will take place more rapidly than when the specimen is not permitted such activity. Although when caged, the females may lay dozens of eggs on one plant, in their natural surroundings the eggs are widely scattered — rarely are two eggs found on a milkweed leaf.

The leaves, bearing the eggs, may be placed in a petri dish or small jar until hatching has taken place. Hatching may be delayed by holding the eggs at a low temperature or accelerated by high temperature.

Potted milkweed plants are desirable for oviposition since they can be left in the cage without deterioration and the larvae will have fresh food available when they hatch. Milkweed can be propagated from seeds or from root stalks, the latter being the quicker method. *Asclepias currasavica* is convenient because it sprouts new shoots readily after the tops have been cut off, and it is easily propagated from stem cuttings.

Since larvae often devour the egg shell upon eclosion they may also devour adjacent eggs. To prevent this, the eggs are separated by cutting the leaves into small fragments, each fragment bearing an egg.

Rearing Containers:

Petri dishes are most suitable for early instars, and glass or plastic jars or tubes for more mature forms. There are many different kinds of containers that are satisfactory for holding large larvae but tight covers are necessary for the smaller ones. When large containers are used, the resulting pupae can be left until the adult butterfly matures. Or, a piece of paper or cardboard can be fastened to the top of the jar and in this way the pupae can be transferred to another jar or cage by simply removing the paper.

When rearing large numbers for migration studies, eggs are placed in wide-mouthed gallon jars with screw tops. When the larvae reach the third instar, they are placed in flight cages. As many as three hundred larvae can be reared in one cage

(Urquhart, 1960). Pupae are formed on the wood frame where they remain until the emergence of the adults.

Flight cages have also been used successfully for rearing large numbers by placing the open end of the cage over a stand of milkweed plants upon the leaves of which a number of larvae have been placed. When the plants have been consumed, the cage is placed over a fresh stand and the larvae transferred.

Food:

Although fresh milkweed leaves, grown in a green house during the winter months, are most effective, frozen leaves, attached to the stalks, which have been thawed, are used successfully. The leaves should be cut before the seed pods are formed — small, young plants being preferred. The thawed leaves may be supported on a wire-mesh platform or hung on the side of the rearing cage. Thawed leaves must be removed daily since deterioration is rapid.

A stand of milkweed can be harvested several times each summer if only the tops of the plants are cut off each time. The old stalk will send out new shoots. If the mature milkweed plants in a field have no insects on them, such as milkweed bugs or beetles, there is a possibility that the field has been sprayed with an insecticide. At least, this possibility should be considered before starting a research project dependent on this source.

To retain the highest nutritive quality in field-cut milkweed, freshly cut stalks, placed in plastic bags, are stored in a field cooler containing dry ice. The bags of milkweed are transferred to a deep freezer refrigerator as soon as possible.

Larvae can be fed on a paste of dried milkweed powder reconstituted with distilled water. Apparently this food is not as stimulating to the appetite or as nutritious as fresh milkweed. The resulting adults, the larvae of which have been so fed, are small, but otherwise normal.

Dale Grisdale (loc. cite) has used an artificial diet, reported by McMorran (1965), with considerable success. Grisdale reports that newly hatched larvae of the Monarch butterfly accepted the food readily and almost one hundred per cent of the larvae established on the food. In order to start the larvae, the artificial food is mixed with powdered milkweed leaves. Without the addition of the powdered leaves, no feeding was evident and all the larvae died during the first instar. He also reports that the adult females were sterile.

Nanavati, working at the University of Delaware, has reared Monarch larvae to adulthood on this medium both with and without the milkweed fraction.

Lyon and Flake (1966) used a similar diet in connection with their studies of the Douglas-fir tussock moth larvae.

E. Alan Cameron of the Division of Entomology, University of California, Berkeley, has used the following diet for rearing the tussock moth. This diet is based on that of Lyon and Flake.

TABLE 1
Composition of Ingredients

<i>Ingredients</i>	<i>Quantity</i>
A.	
Caesin-vitamin free	87.5 g
Alphacel	12.5 g
Salt mixture — W	25.0 g
Sucrose	87.5 g
Wheat embryo	75.0 g
Choline Chloride	2.5 g
Ascorbic acid	10.0 g
Methyl parahydroxybenzoate	3.75 g
Aureomycin	0.75 g
Potassium sorbate	5.0 g
B.	
Water, distilled	550.0 ml.
4 M Potassium hydroxide	12.5 ml.
Vitamin solution	25.0 ml.
Formaldehyde (36%)	1.25 mo
C.	
Nutrient agar	62.5 g
Water	1550 ml.
Mix solution "A" and "B" in blender. Add "C" after melting. Pour into wax-paper lined shallow pans or teflon-coated pans.	

TABLE 2
Vitamin Solution

<i>Ingredients</i>	<i>Quantity</i>
Water	100 ml.
Nicotinic acid (niacin)	100 mg.
Calcium pantothenate	100 mg.
Riboflavin	50 mg.
Thiamine hydrochloride	25 mg.
Pyridoxine hydrochloride	25 mg.
Folic acid	25 mg.
Biotin	2 mg.
Vitamin B-12	0.2 mg.

Disease and Diapause:

Two factors may cause difficulty in rearing the Monarch butterfly successfully throughout the winter months. One is the presence of a virus disease and the other diapause females.

During the past two years ,and commencing three years ago, the natural populations of the Monarch butterfly in North America have been greatly reduced as a result of a polyhedrosis

virus epizootic (Urquhart, 1966). Hence, a high mortality has been experienced in our laboratory cultures regardless of feeding methods used. Even careful sterilization methods have proved ineffective in preventing infection.

It is possible to rear continuous generations of the Monarch butterfly during the winter, starting with eggs of gravid females collected in the field during the summer and fall. Monarch females collected in late September at Cape May, New Jersey, readily laid eggs on milkweed when brought into the Delaware laboratory. No special treatment was necessary. However, at the University of Toronto, it was found that although females collected in the spring and early summer produced continuous generations throughout the winter months migrant females collected in late summer and early fall from over-night roosting sites, did not oviposit even when kept for periods of five months. Similarly, over-wintering specimens from Monterey, California collected from over-wintering sites during December and January would not oviposit. Dissected females collected during January and February from such over-wintering sites rarely contained eggs (Urquhart, 1960). In March, however, many females were gravid prior to their spring migration flight.

Francis Munger, of Whittier, California, who has been working with us at the University of Toronto for the past number of years, reared successive generation of Monarch butterflies throughout the winter months. Larval Monarch butterflies have been sent to us by Miss Martha Lussier of Orlando, Florida, in January.

The possible factors involved in the production of a reproductive diapause in the migrating and over-wintering populations are being studied at the laboratories of the University of Toronto.

Note: Monarch eggs, with which to start a breeding colony, are usually available from Dr. Stegner.

Reprints of this article may be obtained by writing to Dr. Stegner.

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VITAL STAINING OF *COLIAS PHILODICE* AND *C. EURYTHEME*

JOHN M. KOLYER

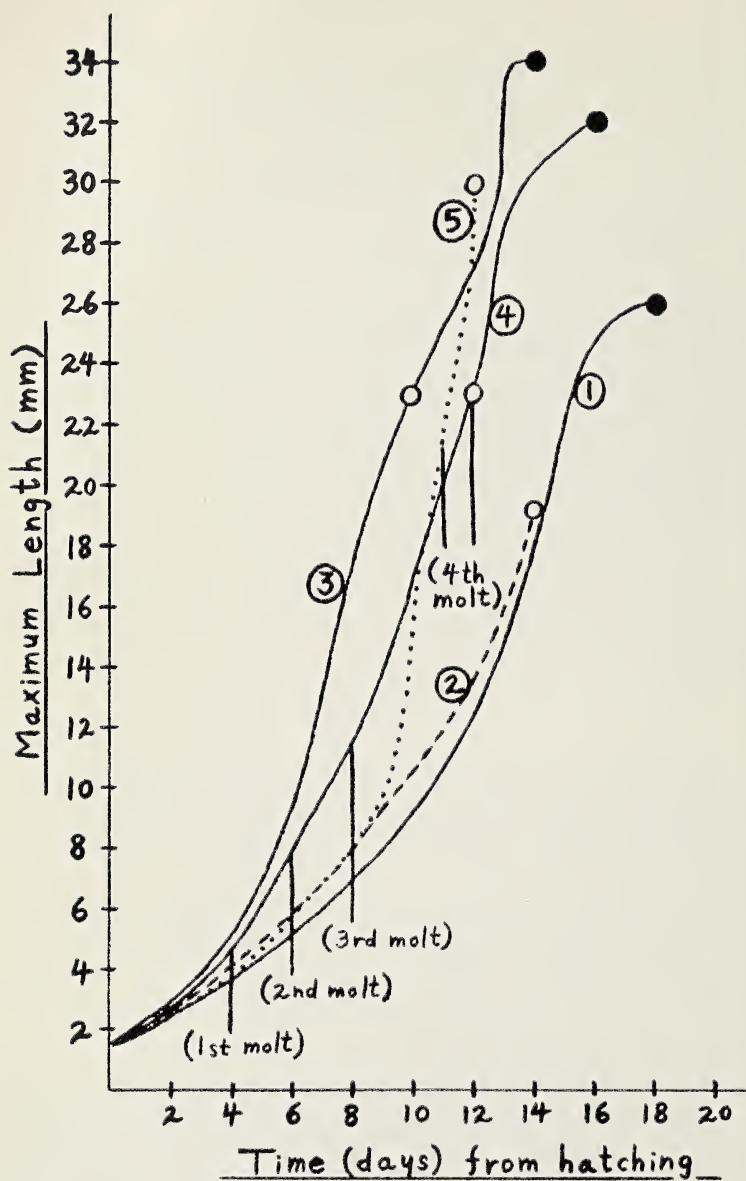
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IN EXPERIMENTS WITH THE LARVAE of *Pieris rapae* (Linnaeus) it was found that ingestion of the dyes neutral red or Nile blue A imparted conspicuous external color (red or blue) to all three stages, while certain other dyes, notably brilliant cresyl blue, gave colored pupae but not adults (Kolyer, 1965). In the present work the three dyes mentioned were tried on the interrelated species *Colias philodice* (Latreille) and *C. eurytheme* (Boisduval) to observe the extent of manifestation of dye color in strongly pigmented butterflies (as opposed to the white *Pieris rapae*), to gain an indication of the generality of the vital staining method, and to optimize the procedure for dye-feeding in the case of the *Colias* species.

REARING

Oviposition. — In all cases the eggs were obtained by confining the female(s) in a screen-covered jar (approximately a cylinder of 3.5 inches inside diameter and 5 inches depth) with a layer of water in the bottom covered by a perforated wire screen through which sprigs of red clover (*Trifolium pratense*) were inserted. Oviposition was stimulated by direct sunlight or by electric light (suitably from a 100-watt bulb ten inches from the jar.) Oviposition began on zero day, and hatching started on the third day for broods 2 and 4 and the fourth day for the other broods (Tables 1 and 2).

Temperature and Humidity. — The broods were reared during July - September, 1962 for brood 1 and July - October, 1966 for broods 2-5. For broods 2-5 the breeding room reached a high of 94°F during the day and a low of 66°F at night, while the relative humidity was in the range 33-70% (usually 40-60%).



Methods for Supplying Leaves. — Both broods (1 and 2) of *Colias eurytheme* were reared on cut leaves of red clover in cardboard boxes, e.g. shoe boxes as mentioned below, with gauze windows in the lids. The difficulty with this method was that rapid desiccation necessitated addition of fresh leaves up to five times a day. Cut leaves of white clover (*Trifolium repens*) were found to lose 50% of their original weight after 20 hours at 73-83°F and 34-45% relative humidity and 73% after 50 hours. To escape this difficulty, the following procedure was used for the three broods of *Colias philodice*. A cardboard shoe box, typically 10 inches long by 4 inches wide by 3.5 inches deep, with perforated bottom and a lid with gauze window, was mounted atop a wide-mouth jar (3.5 inches inside diameter) nearly filled with water, into which white clover stems were inserted. Since the young larvae tended to drop from the leaves when disturbed, the clover leaves at first were situated at some distance from one large perforation by bending over a bundle of stems and taping them to the floor of the box. Later, when the larvae were in the fourth instar, the whole area of the box above the jar was perforated with small holes, and individual stems were inserted to give a "carpet" of clover leaves.

Figure 1 shows that the *philodice* larvae fed by the stems-in-water method developed more rapidly and attained larger size than the *eurytheme* larvae fed cut leaves. Klots (1951) lists a greater maximum expanse for *eurytheme* (2.4 inches) than for *philodice* (1.9 inches), and the forewing length for females collected in the general vicinity of Morristown, New Jersey, was greater for *eurytheme* (29 mm, mean of seven specimens) than for *philodice* (26 mm, also mean of seven specimens). Also, the larva of *eurytheme* has been described as attaining a slightly greater length than that of *philodice* (Comstock and Comstock,

Fig. 1. Growth curves for larvae of broods 1-5.

The curves are identified by brood no.; see Tables 1 and 2. The open circles mark the beginning of dye-feeding. In the case of broods 3 and 4 some readings were taken beyond this point, but these are not equivalent to the preceding values and are plotted only to show the greater length attained and more rapid development of these broods (vs. 1 and 2) even with the retarding effect of dyes.

The solid circles mark the beginning of pupation.

Maximum larval length was noted daily and plotted vs. time, and smooth curves were drawn through the points. In actuality there are short no-growth steps, especially preceding the fourth molt. Approximate positions of the molts are indicated on the graph for brood 4 (and the fourth molt of brood 5).

As a weight reference, two 25 mm larvae from brood 1 weighed 0.180 and 0.213 grams.

Table 1
CONDITIONS FOR DYE-FEEDING

Brood No.	Colias Species	Dye (% of blend)	Feeding Start Length, mm	Time, day	Time Dye Fed, days	Pupation, day	Yield Pupae	Color Pupae
1	<u>surriana</u>	none	-	-	-	23-31	(34 from 65 1st-instar larvae)	green
2	<u>surriana</u>	Mile blue A (5)	22-24	20-21	1.5-1.8	22-27	10/10	one blue (15 mm), rest sl. blue-green at most
		neutral red (5)	19-24	17-21 ¹	5	23-26	7/9	pink (esp. on abdomen) to deep red
		Mile blue A (1) and neut. red (1)	22	21 ¹	3-5	24-26	5/5	green to green with blue abdomen
		brill. cre-syl blue (5)	18-20	21 ¹	4-5	25-26	3/3	green
3	<u>philodice</u>	Mile blue A (5)	15-23	14	0.8-1.4	18-19	4/20	blue-green ²
		Mile blue A (1)	24-27	16	2.3-4.5	20-22	2/8	greenish-blue; blue
		(1) neutral red (5)	15-19	14 ¹	4-5	18-19	7/10	dark-red
		(2) neutral red (5)	26-30	18	0.5	20-21	3/3	two dark-red; one green with red abdomen
		Mile blue A (1) and neut. red (1)	17-19	15	0.5	19	4/5	sl. blue tint
		brill. cre-syl blue (5)	18-19	15 ¹	3-4	18-19	4/4	sl. grayish green
4	<u>philodice</u>	neutral red (5)	28-32 (one at 24)	16-19 ¹	0-3	19-21	32/32	red to dark-red
5	<u>philodice</u>	Mile blue A (1)	27-30	16-17 ¹	2-3	18-20	4/10	blue-green

¹red dye to pupation. ²green for controls.

1943). Therefore, it seems reasonable that *philodice* is not inherently larger than *eurytheme* but, if anything, smaller, and that the improved rearing procedure was responsible for the more rapid growth rates and greater ultimate lengths of the *philodice* larvae as well as the greater expanse of the adults (See forewing measurements in Table 2).

Mortality seemed reduced by the improved feeding method; for example, in brood 4, 39 eggs yielded 34 larvae which yielded 32 adults, while in brood 1 (cut leaves) 65 first-instar larvae (from approximately 150 eggs) yielded only 34 pupae, and in brood 2 (also cut leaves) only 34 larvae remained of the original 54 (from about 111 eggs) when the largest had reached 19 mm. No crowding problem was evident in brood 4 when the newly-hatched larvae (34) were reared to give 33 fifth-instar larvae (29 mm maximum length) in a single box of dimensions specified above.

Dye-Feeding Technique. — Dyes were fed by coating the leaves on both sides with dye-mica blend prepared by grinding and tumbling the dye with P-12 Davenite mica (325 mesh; Hayden Mica Co., Wilmington, Mass.) as described in the earlier paper (Kolyer, 1965). However, the dye/leaf ratio in the present work was higher than with *Pieris rapae* because more dye blend was used (about 5 mg for a white clover leaf 1.5 cm wide) and because clover leaves are far less thick than the average cabbage leaf.

The dyes (biological stains), all from National Aniline Division, Allied Chemical Corp., New York City, were brilliant cresyl blue (Colour Index No. 51010), neutral red (chloride, 70% minimum strength, 1.0% maximum water-insoluble content, Colour Index No. 50040), and Nile blue A (sulfate, 70% minimum strength, Colour Index No. 51180).

Explanation of Table 1. — The days listed for inception of dye-feeding, pupation, and eclosion in the tables are all based on the start of oviposition, which continued no more than three days, at zero day. In the Yield Pupae column, 7/9, for example, means that 7 pupae were obtained from 9 larvae fed dye. The pupal color was noted when pupae were about two days old.

Description of Female Parents. —

Brood 1. — Eggs (approximately 150) were laid by one *eurytheme*, moderately marked with orange, forewing 23 mm, taken near Fall River, Mass., on July 22, 1962.

Brood 2. — Eggs (approximately 111) were laid by some or all of five *eurytheme*, most by one moderately marked with orange,

Table 2

Brood No.	Dye (% of blend)	Ecdlosion, day	Color Pup- pal Case	DATA ON ADULTS		Forewing Length, mm, span (range)	Ground Color	Eye Color	Color Inter- segmental Abdominal Membrane	
				No. of Adults						
				male	female					
1	none	29-38	pale yellow	15	14	male-21(20-23) female-22(20-24)	orange	lt. green	lt. green	
2	Mile blue A (5)	28-33	pale blue	6	4	male-19(15-22) female-23(21-24)	orange ¹	deep green	blue	
	neut. red (5)	28-32	pink	5 ²	0	male-18(15-21) female-23(21-24)	orange; deep orange for unexpanded specimens	golden-brown	pink	
	Mile blue A (1) and neut. red (1)	30-33	pale blue	1	4	male-18 female-20(18-23)	orange	lt. green	blue	
	brill. cre- syl blue (5)	31-32	pale yellow	1 ³	1	male-20 female-20	orange	lt. green	lt. green	
	none (control)	32-33	pale yellow	3	2	male-22(21-24) female-24(23,24)	orange	lt. green	lt. green	
3	Mile blue A (5)	23-25	pale greenish- yellow	2	2	male-23(22,23) female-27(26,28)	faint green tint (1 male)	green	blue	
	Mile blue A (1)	26-29	pale greenish- yellow	1	1	male-21 female-21	faint green tint in male	green	blue	
	(1) neut. red (5)	23	pink	1 ⁴	0	-	orange	red	deep-red	
	(2) neut. red (5)	25-27	flesh-color	1	2	male-23 female-26(25,26)	sl. deeper yellow to orange-tan	golden- yellow to yellow-red	red	
	Mile blue A (1) and neut. red (1)	24-25	pale yellow	0	4	female-27(26-29)	yellow	lt. green to green	blue	
	brill. ore- syl blue (5)	23-25	pale greenish- yellow	1	3	male-20 female-22(21-23)	yellow	lt. green	gray	
	none (control)	24-25	pale yellow	0	3	female-29(28-29)	yellow	lt. green	gray	
4	neut. red (5)	25-29	flesh-color	12	9Y ⁵ 11A ⁵	male-23(20-25) female-24(23-26)	Y-orange-tan A-pink	Y-golden to deep-red A-deep-red	red	
5	Mile blue A (1)	24-25	pale blue or greenish-blue	2	1	male-21(21,21) female-21	yellow-green (males), pale blue (albino female)	green	blue	

¹one sl. greenish inside border; see Plate 1. ²two failed to expand.³another eclosed but not expanded. ⁴not expanded. ⁵Y means yellow; A means albino.

forewing 26 mm, taken at Berkshire Valley, New Jersey, on July 3, 1966.

Brood 3. — Eggs (81) were laid by three *philodice*, wings yellow with no trace of orange, forewings 24, 26, 27 mm (mean 26 mm) taken at Morristown, New Jersey, on July 12 and 13, 1966.

Brood 4. — Eggs (39) were laid by three albinos, presumably *philodice* (as judged by width of the black borders of the forewings) with no trace of yellow or orange in the ground color, forewings 24,25,26 mm (mean 25mm), taken at Berkshire Valley, New Jersey, on September 3, 1966.

Brood 5. — Eggs (11) were laid by an albino female with a touch of yellow-orange in the wings, forewing 25 mm, and/or a yellow *philodice*, no trace of orange, forewing 27 mm, both taken at Morristown, New Jersey, on September 10, 1966.

RESULTS

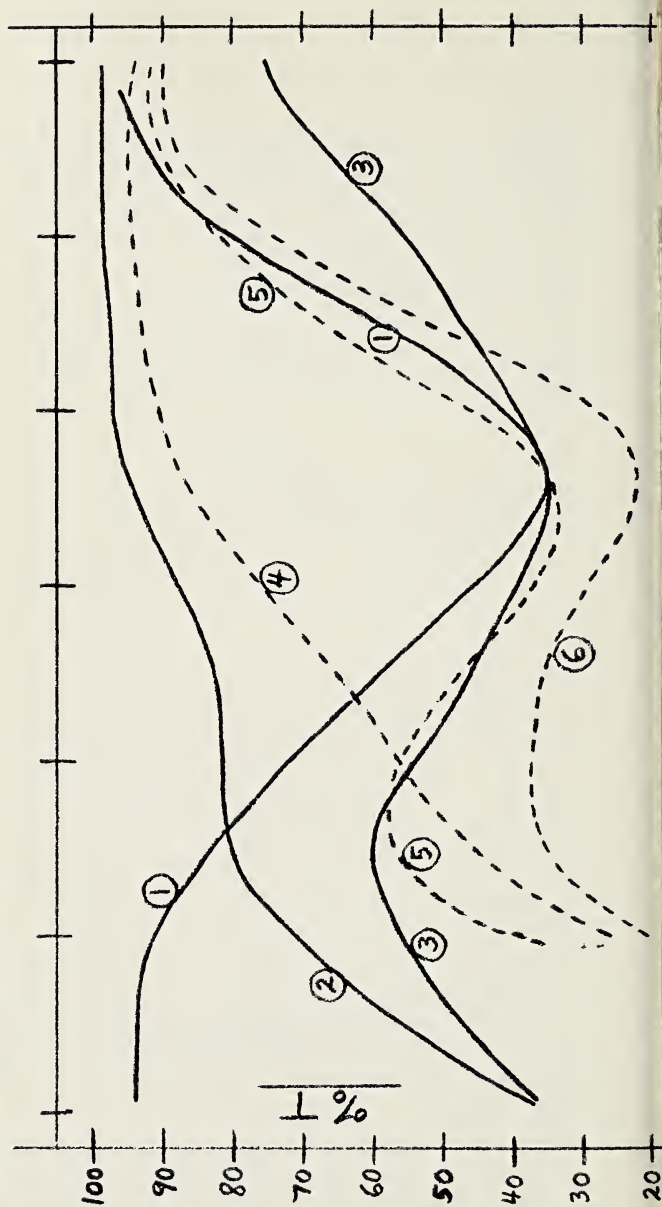
Color of Adults. — The situation is complicated by the fact that *philodice* and *eurytheme* are peculiarly interrelated and hybridize to some extent; see, for example, Gerould (1946) and Hovanitz (1949). However, the adults reared in broods 1 and 2 were typical *eurytheme*, well marked with orange, while the undyed adults reared in brood 3 were all typical *philodice*, like the parent females, with no trace of orange. In brood 5 the female was an albino, and the males appeared to be typical *philodice*. Only in brood 4 among the *philodice* broods was there a trace of *eurytheme*; a male and female which pupated without feeding on the dye (neutral red) showed a faint orange suffusion in the basal area of the forewing, and this could be observed in some of the dyed specimens (except the albinos, which were evenly pink like dyed *Pieris rapae* and presumably would have been quite uncolored if not fed neutral red). The introduction of color solely by neutral red as opposed to *eurytheme* genes seems unequivocal in brood 3, in which all 17 adults except the four fed neutral red (e.g., no. 6, Plate 2) were quite yellow (with very faint greenish tint in some of the six fed Nile blue A). Approximately half the females in brood 4 were albinos, which form is known to be controlled by a dominant allele (for example, Hovanitz, 1944).

The color of the antenna club was altered by dye-feeding. This was tan in the controls (either species) and in specimens fed brilliant cresyl blue but was deep-green when Nile blue A had been fed and red-brown when neutral red had been fed (orange

Fig. 2. Spectra of extracts of adults stained with neutral red.

All spectra are for extracts of *Colias philodice* specimens. Spectra 4-6 were run at greater sensitivity than 1,2,3,7, and 8, and 9-11 were run at still greater sensitivity. % T = percent transmittance.

1 — neutral red (12 mg/l) in 1.20 ml concentrated hydrochloric acid (37-38% HCl) plus 3.75 ml concentrated ammonium hydroxide (28-30% ammonia); 2 — extract of body (36.5 mg) of albino female; see text for extraction procedure; 3 — extract of body (26.6 mg) of pink albino female; fed neutral red (brood 4); resembled no. 2, Plate 1). 4 — extract (boiling water) of whole albino female (46.9 mg); see text for procedure. 5 — extract (boiling water) of whole pink albino female (39.1 mg) fed neutral red (brood 4). 6 — extract (boiling water) of whole albino female (spectrum 4), with neutral red added at 0.028 mg/7.0 ml extract. 7 — neutral red spectrum (1) and albino body spectrum (2) combined by adding optical densities. 8 — extract of albino female body (spectrum 2) with neutral red added at 0.055 mg/4.95 ml extract. 9 — extract of albino female forewing; see text for procedure. 10 — neutral red spectrum (at appropriate concentration) and albino forewing spectrum (9) combined by adding optical densities. 11 — extract of forewing (2.0 mg) from pink albino female fed neutral red (brood 4).



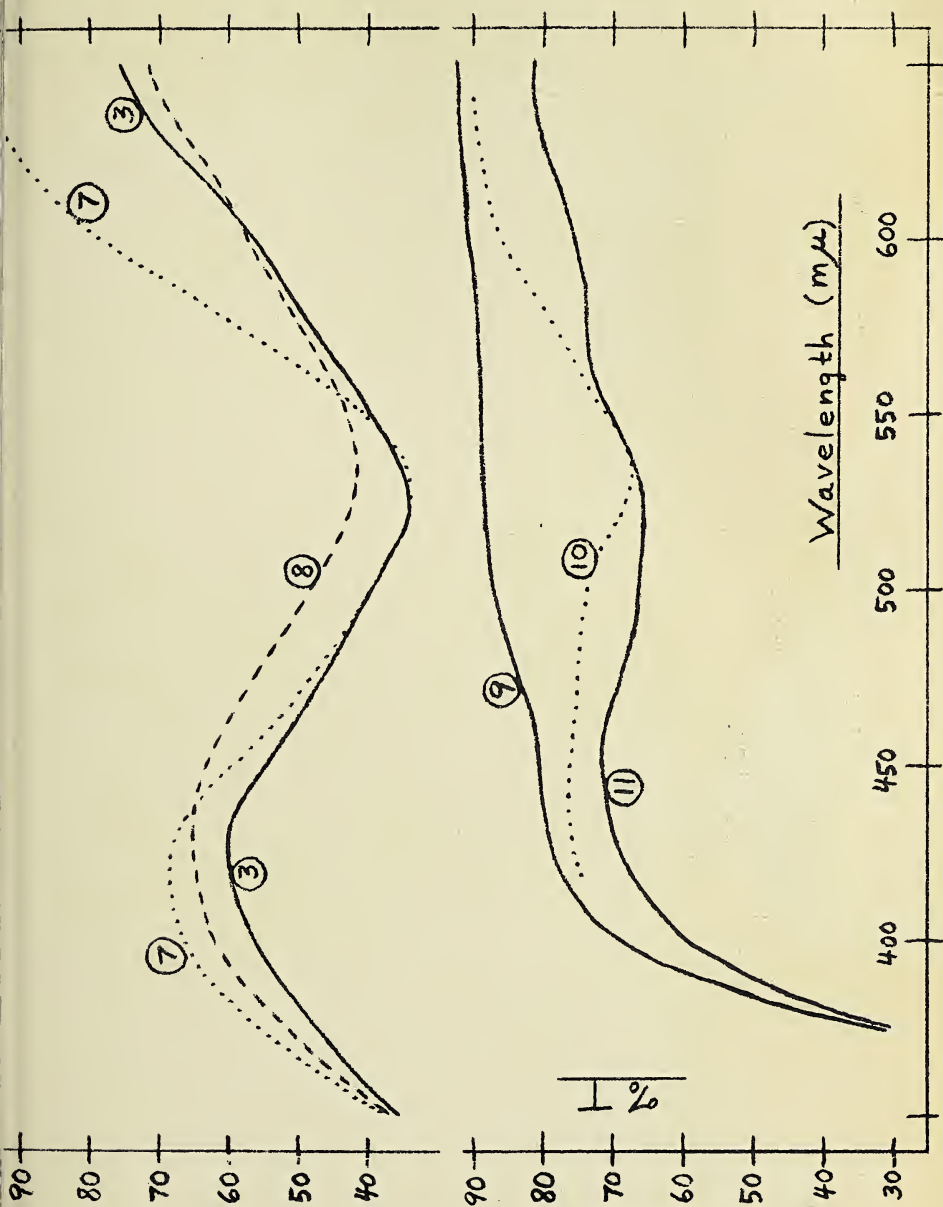




PLATE 1. SPECIMENS STAINED WITH NILE BLUE A AND NEUTRAL RED BY FEEDING DYES TO THE LARVAE.



PLATE 2. SPECIMENS STAINED WITH NEUTRAL RED BY FEEDING THE DYE TO THE LARVAE.

1 — male *Colias eurytheme*, forewing 15 mm, fed Nile blue A, brood 2, from blue pupa (length 15 mm vs. normal length of 20 mm); 2 — albino female *C. philodice* fed neutral red, brood 4. 3 — albino female *C. philodice* fed Nile blue A, brood 5. 4 — male *C. philodice* fed Nile blue A, brood 5. 5 — female *C. philodice* control, brood 3. 6 — female *C. philodice* fed neutral red, brood 3. 7 — male *C. philodice* fed neutral red, brood 4. 8 — female *C. philodice* fed neutral red, brood 4.

The pupal case is shown with each specimen.

in the case of albino females).

The liquid voided following eclosion was blue-green for adults fed Nile blue A and strongly red for those fed neutral red.

Verbal description of color is vague at best (and photographic reproduction is hardly accurate), but the direction of vital staining should be evident from Table 2 as well as Plates 1 and 2.

Explanation of Table 2. — Forewing length is the distance from the base to the apex of the wing. The eye color was noted on living adults with the aid of a 16-power stereo microscope. The color of the abdominal membrane was observed by flexing the abdomen of a living specimen under the microscope to separate the segments. This was a sensitive indicator of the presence of Nile blue A or neutral red.

Concentration of Neutral Red in Adults. —

Paper Chromatography on Wings. — Single forewings were extracted by grinding the wing in a mortar with 1.0 ml concentrated hydrochloric acid (37-38% HCl). The liquid and undissolved debris were transferred with about three ml distilled water to a watchglass and evaporated to dryness on a hot plate. The soluble part of the residue was taken up in 0.15 ml distilled water and chromatographed by the ascending method (for a general description see Lederer and Lederer, 1953). Whatman No. 1 filter paper (3 inches by 4.5 inches) was made hydrophobic, in the manner of Ciglar, Kolsek, and Perpar, 1962, by dipping in 10% lauryl alcohol in 95% ethanol and allowing to dry. Spots (about 3 mm diameter) were applied with a capillary 5/8 inch from the shorter edge of the paper; three applications were made, with drying between, to reinforce each spot. The paper was dipped, spotted edge down, to a depth of 1/4 inch in a layer of solvent (2 volumes 95% ethanol : 2 volumes concentrated ammonium hydroxide (28-30% ammonia) : 1 volume distilled water) in a closed jar and left for one hour at room temperature (27°C). After drying in a draft of air the chromatogram was sprayed with 1.5% aqueous HCl to bring out the pink spot for neutral red.

For a female *philodice* fed neutral red (brood 4, resembling no. 8, Plate 2) the tan spot, Rf 0.75, due to wing pigments, was well separated from the pink spot, Rf about 0.24, for neutral red; wings of undyed *philodice* or *eurytheme* gave only the tan spot, as expected. Several quantities of neutral red (from same sample used to prepare the blend with mica) were evaporated with concentrated hydrochloric acid and chromatographed in the same way to allow a semiquantitative estimation of neutral red level in the wing by comparison of spot intensities. The result was very

approximately 0.01 mg neutral red, or, since the wing weighed 2.0 mg., 0.5% neutral red in the wing. The dye seems confined to the scales, incidentally; the membrane is colorless.

Colorimetry. — A Bausch and Lomb Spectronic 20 Colorimeter (band pass 20 millimicrons) was used to take % transmittance readings (readily converted to optical density, which equals the negative logarithm, to the base 10, of the transmittance) at every 10 millimicrons (in regions of absorption maxima) in the range 350-650 millimicrons (3500-6500 Angstroms). The % transmittance was readjusted to 100 with solvent at each wavelength. The sensitivity setting of the instrument was varied from nearly a maximum level for the wing extracts to lower levels for the other determinations. The spectra within each of the three sets were run at the same sensitivity and included standard neutral red solutions for calibration.

Body. — The body of a dried specimen (wings removed) was ground in a mortar with 1.20 ml concentrated hydrochloric acid (37-38% HCl), and the mixture was partly neutralized (to pH about 0.3) by adding 3.75 ml ammonia solution prepared by diluting one volume concentrated ammonium hydroxide (28-38% ammonia) to five volumes with distilled water. Debris was removed by filtration. The spectra of dyed and undyed albino bodies (nos. 2 and 3) are shown in Figure 2 as well as the spectrum of neutral red in the same solvent. The absorption maximum for neutral red was 530 millimicrons, as has been reported for acid solutions (Meyer and Treadwell, 1952), and a calibration curve (optical density vs. concentration) was obtained for this wavelength using several neutral red concentrations. By summing the optical densities of spectra 1 and 2, the predicted spectrum (neutral red superimposed on the undyed albino body extract) was obtained (no. 7). This was a fair match for the actual spectrum of the dyed albino (no. 3) except for considerable deviation above 550 millimicrons. However, addition of the amount of neutral red (as a concentrated solution) predicted for the dyed albino body by means of the calibration curve to the undyed albino body solution gave spectrum 8, which is in rather good agreement with the spectrum of the dyed albino body over the whole wavelength range. Since the level of neutral red in the extract of the dyed albino body was 0.066 mg (after correcting for the difference between spectra 8 and 3) and the body weighed 26.6 mg, the neutral red extracted amounted to 0.25% of the body. This is about double the level for the living body, since this species should lose about half its original weight on

drying (Kolyer, 1963).

Whole Adult. — The whole (dried) butterfly was ground in a mortar with about 5 ml acetone, transferred to a flask with about 25 ml acetone, and refluxed for 20 minutes with the intention of degreasing the body. Then the acetone was evaporated and replaced by about 10 ml distilled water. After refluxing for 30 minutes (neutral red is not affected by this treatment), the mixture was evaporated to about 4 ml, 0.035 ml concentrated hydrochloric acid was added, and the mixture was diluted to 7.0 ml with distilled water and filtered to remove debris. In Figure 2, spectra 4 and 5, respectively for undyed and dyed albinos, are generally similar to spectra 2 and 3 for the bodies. Addition of neutral red to the undyed albino extract gave spectrum 6, and the calibration curve indicated 0.022 mg in the extract or 0.06% neutral red in the butterfly. A dyed (orange) female (brood 4, resembling no. 8, Plate 2) and an undyed yellow female gave rather similar spectra to those for the albinos, and the neutral red level was the same (0.06% of the dyed butterfly, which weighed 37.0 mg). The low results suggest that this extraction method was less effective than trituration with concentrated hydrochloric acid, which dissolves much of the specimen.

Wing. — Single forewings were extracted in the same manner as the bodies (above). As in the case of the bodies, the calculated spectrum for the dyed albino (no. 10 in Figure 2) deviated from the observed spectrum (no. 11) above 550 millimicrons. By subtracting the optical density of spectrum 9 (undyed albino) at 530 millimicrons from that of spectrum 11 and converting to neutral red concentration by means of a calibration curve, a value of 0.0036 mg was found for the forewing of the dyed albino; this is 0.18% of the wing, which weighed 2.0 mg. Similarly, 0.0038 mg neutral red (0.19% of the wing) was found for the forewing of a dyed (orange) female from brood 4 resembling no. 8 in Plate 2. Incidentally, the spectrum of the extract of an undyed, yellow *philodice* wing showed 24% transmittance at 400 millimicrons and rose to a plateau of about 79% by 570 millimicrons, while an undyed *eurytheme* wing was less transparent in the lower (blue) region (12% transmittance at 400 millimicrons) and more transparent (e.g. 90% transmittance at 590 millimicrons) in the yellow and red regions. This is consistent with the presence of orange pigment.

Concentration of Nile Blue A in Adults. — No assay was made on the three *philodice* specimens conspicuously colored by Nile blue A (brood 5). However, the intensity of this dye is com-

parable to that of neutral red; for solutions of equal weight concentration neutral red gave optical density 0.27 at 530 millimicrons vs. 0.41 for Nile blue A at its maximum of about 640 millimicrons (Merrill and Spencer, 1948, report 634 millimicrons). Therefore, visual estimation suggests a concentration of on the order of 0.1% Nile blue A in the wings of the dyed albino from brood 5 (no. 3 in Plate 1).

DISCUSSION

Effect of Dyes on the Colias species vs. Pieris rapae. — The toxicity of Nile blue A was more pronounced with the *Colias* species than *Pieris rapae* when the level ingested was high enough to alter the wing color conspicuously. In brood 5, three well-dyed specimens were obtained (two shown in Plate 2) only at the expense of 70% mortality. As with *Pieris rapae*, Nile Blue A preferentially showed itself in *Colias* adults (abdominal membrane) when fed with neutral red at equal levels (Table 2).

Neutral red gave strongly pink specimens with 30% mortality with *Pieris rapae* (Kolyer, 1965), and good coloration with no mortality was achieved with *Colias philodice* (brood 4) when feeding was begun at the proper larval length.

Brilliant cresyl blue gave strongly violet pupae when fed to *Pieris rapae* larvae for 3-9 days, but when fed (at a higher dye/food ratio) to *Colias philodice* for 3-4 days (brood 3) there was only a subtle change in pupal color (Table 1). A feeding period of 4-5 days had no noticeable effect on the color of *C. eurytheme* pupae (brood 2). It is interesting that this dye gave very different results for *Pieris* vs. *Colias*.

Toxicity and Growth-Retarding Effect of Dyes. — Brilliant cresyl blue may have shown a slight retarding effect on the *Colias* species, while Nile blue A was toxic to the point of being very "tricky" to utilize and, besides killing larvae, produced some undersized specimens, the smallest being the dwarfed male shown in Plate 1.

Neutral red retarded growth and had a toxic effect in *C. eurytheme* when feeding was begun too early; a dwarfed male with 15 mm forewing was produced in brood 2, and only three properly-expanded adults were obtained from nine larvae. In this case the ground color was noticeably changed only in the unexpanded specimens, presumably because it was difficult for neutral red to manifest itself against the orange pigment. With *C. philodice*, larval growth was retarded (maximum length attained was 27 mm) and undersized, deformed pupae resulted

when neutral red feeding was begun too soon (group(1) in brood 3). However, when feeding was begun (brood 4) with larvae that had attained 83-94% of the ultimate length for controls (34 mm), there were no deaths, and only about five specimens out of 31 were not well tinged with pink. A single specimen (brood 4) fed neutral red from a length of 24 mm (71% of ultimate length) eclosed but failed to expand. It should be noted that staining with neutral red is reversible with *Colias* as with *Pieris rapae* and the silkworm (Edwards, 1921); loss of dye begins when the larva is transferred to undyed leaves. This effect is avoided, of course, by feeding the dye to pupation.

Optimum Dye-Feeding Procedure. — In agreement with the cited work with *Pieris rapae*, neutral red is judged particularly suitable for vital staining of the *Colias* species. The best procedure (at the level used in the experiments) is to confine dye-feeding to the latter part of the final instar. Alternatively, it is possible that the dye might be fed earlier if used at a lower concentration; a brief experiment with 1% neutral red in the blend showed that the larvae were visibly stained (as indicated conveniently by change in color of the lateral stripe) after being fed dye for 12 hours.

CONCLUSION

Neutral red has been found to be an effective vital stain, with an acceptable degree of toxicity, in *Pieris brassicae* (linnaeus) (Roer, 1959), *Pieris rapae* (Kolyer, 1965), the *Colias* species (present paper), and also the silkworm (Edwards, 1921). Vital staining provides indelible marking, which might be of use in the rearing of experimental broods, but an area of more interest might be the effect of the unusual color on the behavior, e.g. mating, of adult butterflies. The concentration of dye in the adult eye might alter response to light, for example; this has been suggested as an area for experimentation with moths fed rhodamine B (Vail, Howland, and Henneberry, 1966).

SUMMARY

Nile blue A and neutral red can be used to stain living larvae, pupae, and adults of *Colias philodice* and *eurytheme* by feeding leaves coated with dye extended with powdered mica. The usefulness of Nile blue A is limited by its toxicity, but neutral red is effective with little or no mortality when fed to larvae within

two or three days of pupation. The wings of yellow *Colias philodice* adults were stained by neutral red to a dull orange color, while dyed albinos were strongly pink. Paper chromatography and colorimetry on extracts of dried specimens indicated a level of on the order of 0.2-0.5% neutral red in the wing and 0.3% in the dried body. Brilliant cresyl blue, which is effective in staining the pupa of *Pieris rapae*, had little efficacy with the *Colias* species.

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THE NORTH AMERICAN SPECIES OF THE GENUS *ZEIRAPHERA*

TREITSCHKE (OLETHREUTIDAE)

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THE NORTH AMERICAN SPECIES OF *ZEIRAPHERA* feed almost entirely on conifers of the tribe Abietae. The only exception is *Z. claypoleana* (Riley) which feeds on *Aesculus* and is morphologically remote from the others. Many of the species occur abundantly enough to be of economic importance and because of this the Forest Insect and Disease Survey, Canada Department of Forestry and Rural Development, has been conducting investigations on them for several years. One result has been the accumulation of about 1400 specimens reared from various conifers in many areas of Canada. The taxonomic study of these forms the basis of this paper.

The specimens were divided in accordance with their respective host trees and geographical areas. A close examination of the maculation and genitalia showed that seven conifer-feeding species are present. Some of these are very closely related but all can be recognized by differences in maculation and in the genitalia. These differences are not always apparent unless examined in series. We have, therefore, usually illustrated the male genitalia of several specimens of each species to show the variation within the species and the differences between them.

A comparison of the North American species with the conifer-feeders of Europe showed that differences exist between them. It has therefore been concluded that the European species *Z. diniana* (Guénee) and *Z. ratzeburgiana* (Ratzeburg) do not occur in North America. *Z. improbana* (Walker) is used for *Z. diniana* of American authors. The North American species formerly considered as *ratzeburgiana* is described below as *canadensis* new species.

GENITALIC DEFINITION OF ZEIRAPHERA TREITSCHKE

Zeiraphera Treitschke, 1829, *Schmett. Europa* 7: 231.

Type species: *Tortrix corticana* Hübner, 1811, *Europa Schmett.* Pl. 3, fig. 13 [= (*Pyrallis*) *Zeiraphera isertana* (Fabricius) 1793, *Ent. Syst.* 3: 281; designated by Curtis, 1838, *British Ent.* 15: No. 711.]

Male genitalia. Clasper sickle-shaped; ventral margin spined; apical region tongue-shaped; sacculus not spined; margin between sacculus and apical region not strongly concave. Uncus rudimentary; with specialized scale-like hairs. Socii well developed, long, drooping, broad. Gnathos weakly developed. Aedeagus short, moderately stout; cornuti a cluster of 3-60 elongate spines.

Female genitalia. Eighth, ninth, and tenth abdominal segments very long and slender. Ovipositor retractile. Anterior and posterior apophyses long. Ostial plate arising from near bases of anterior apophyses, elongate, emarginate basally. Ostium somewhat cup-shaped. Ductus bursae constricted; entirely sclerotized, with sclerotized ring only, or membranous. Bursa with one of two scobinate signa.

Key to Species

1. Female bursa with one signum (Fig. 34). Male clasper without subapical constriction (Fig. 32) 2
 Bursa with two signa (Fig. 37). Clasper with subapical constriction (Fig. 26) 6
2. Signum very small (Fig. 35). Ductus bursae membranous. Forewing with an oblique, rectangular, whitish grey patch near middle of dorsum (Figs. 23-24). Hosts: *Picea sitchensis*, *P. engelmanni* 8
 vancouverana McD.
- Signum of moderate size (Fig. 40). Ductus bursae weakly sclerotized .. 3
3. Uncus well developed (Fig. 29). Forewing with indistinct maculation and dorsal patch (Figs. 7-11). Hosts: *Larix laricina*, *L. occidentalis* 4. *improbana* (Wlk.)
 Uncus weakly developed (Fig. 30) 4
4. Frons and vertex whitish ochreous. Forewing with a distinct, white, median band not constricted near middle and containing a longitudinal, shining, pale ochreous line (Figs. 12-14). Hosts: *Picea glauca*, *P. engelmanni* 5. *fortunana* (Kft.)
 Frons and vertex greyish brown 5
5. Whitish median band of forewing constricted near middle or separated into a costal and a dorsal patch (Figs. 15-18). Hosts: *Picea glauca*, *P. sitchensis*, *P. engelmanni*, *P. mariana*, *Abies lasiocarpa*, *A. balsamea*, *A. amabilis* 6. *destitutana* (Wlk.)
 Forewing with a distinct, whitish, semi-circular dorsal patch (Figs. 19-22). Hosts: *Pseudotsuga menziesii* 7. *hesperiana* n. sp.
6. One signum broader than the other 7
 Signa almost equal in size 8
7. Neck of bursa with a slender sclerotized ring (Fig. 38). Ostial plate broad. Forewing with a pale brown, triangular, dorsal patch mixed with white scales (Figs. 3-4). Wingspread 12-15 mm. Hosts: *Picea glauca*, *P. sitchensis* 3. *canadensis* n. sp.
 Neck of bursa with a broad sclerotized ring (Fig. 36). Ostial plate slender

der. Forewing with greenish, blackish, and whitish areas. Male with an indistinct, green dorsal patch; female with a large, blackish dorsal patch (Fig. 2). Wingspread 14-16 mm. Host: *Aesculus glabra* 1. *claypoleana* (Riley)

8. Neck of bursa with a slender sclerotized ring. Forewing with a golden dorsal patch edged with white scales (Figs. 5-6). Wingspread 12-16 mm. Host: *Picea sitchensis* 2. *pacifica* Free.

1. *Zeiraphera claypoleana* (Riley)

Sericorsis instrutana: Claypole, 1881, *Proc. Am. Assn. Adv. Sci.* 30: Riley, 1881, *Am. Nat.* 25: 1009.

Proteoteras claypoleana Riley, 1882, *Amer. Midland Nat.* 10: 913; Forbes, 1923, *Cornell Univ. Agric. Exp. Sta. Mem.* 68: 440.

Steganoptycha claypoleana (Riley), Claypole, 1882, *Psyche* 3: 364; Riley, 1883, *Papilio* 3: 191; Packard, 1890, *Fifth Rept. U.S. Ent. Comm.* 654; Lintner, 1897, *Rept. N. Y. State Ent.* 12: 214.

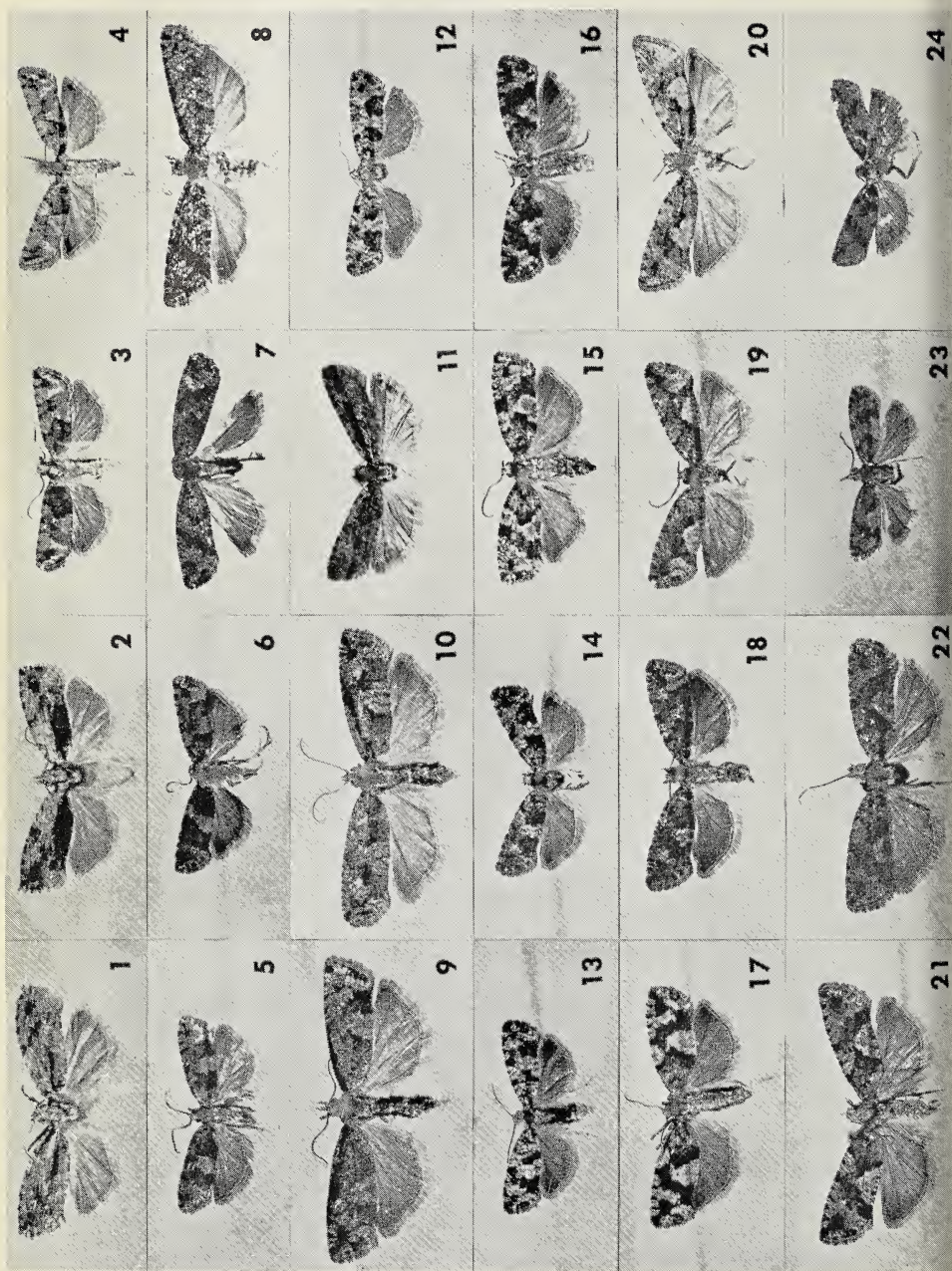
Epinotia claypoleana (Riley), Fernald 1917, in *Dyar List N. Am. Lep.* No. 5232.

Zeiraphera claypoleana (Riley), Heinrich, 1923, *Proc. U. S. Nat. Mus. Bull.* 123: 170.

External characters. Frons fawn colored; roughly scaled. Vertex with long, light fuscous scales mixed with whitish ones. Antenna with light brown and fuscous scales; scape whitish outwardly. Palpus whitish inwardly, brownish fuscous with some whitish scales outwardly. Thorax whitish brown with two lateral, blackish-fuscous spots. Base of tegula blackish. Abdomen pale brown. Legs pale fuscous; fore- and mid-tarsi fuscous with paler bands. Male forewing (Fig. 1) with basal patch whitish on costal half, blackish brown at middle and greenish on dorsum; median band whitish, extending obliquely outward from costa to middle of wing, then acutely angling inward to dorsum, costal portions obscure; apical third whitish, with a brown subapical spot and three brown costal spots; fringe whitish fuscous, with three subapical white dashes. Hind wing pale fuscous; fringe whitish fuscous. Female forewing (Fig. 2) with a large blackish-brown dorsal patch; post-median area and subapical spot greenish. Wingspread 14-16 mm.

Male genitalia (Fig. 25). Uncus pointed at apex. Socii well developed, broadly sickle-shaped. Tegumen obtusely angled. Clasper arcuate, long, slightly expanded at apex, somewhat concave ventrally near base, densely spined. Sacculus weak. Aedeagus short, stout, broader at base; cornuti a cluster of about 20 long spines.

Female genitalia (Fig. 36). Apical region of anterior apophyses expanded. Ostial plate slender, strongly emarginate. Ostium small, cup-shaped. Ductus bursae with a small sclerotized plate. Neck of bursa with a broad sclerotized ring. Signa two, unequal in size, conical.



Flight period. June.

Type locality. Ohio.

Distribution. Ohio, Missouri, Texas.

Host plant. *Aesculus glabra* Willd.

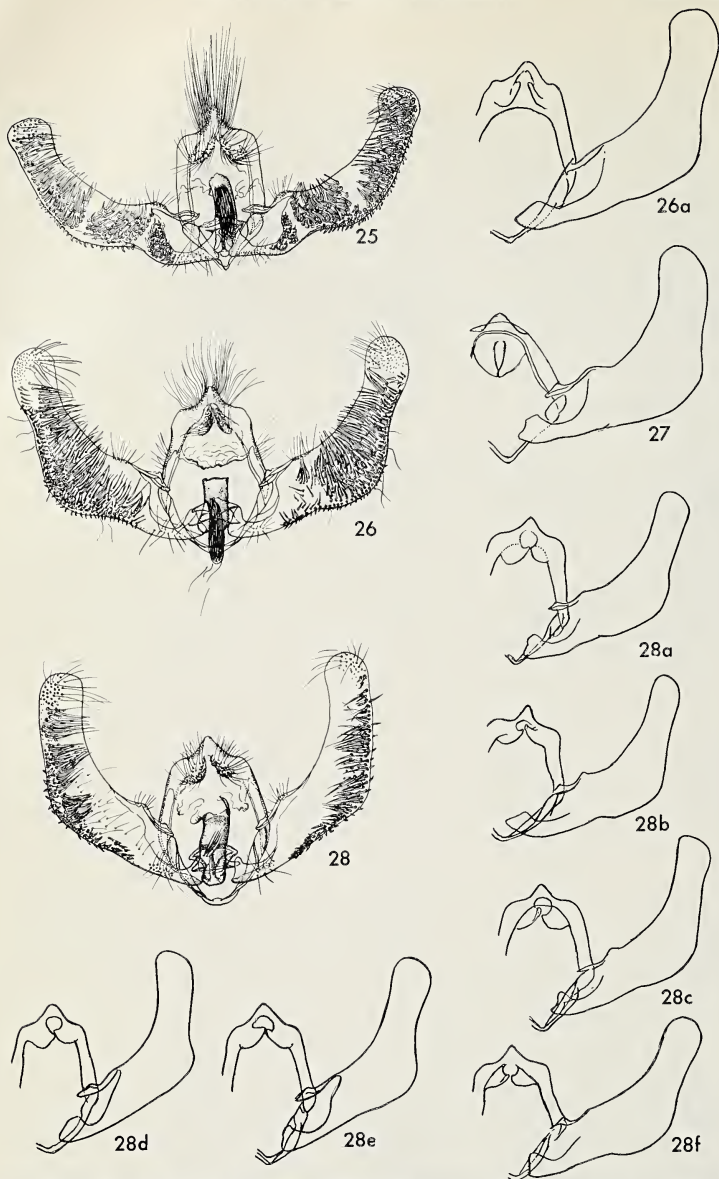
Remarks. This species was placed in this genus provisionally by Heinrich (1923) on the basis of similarities in the male genitalia. However, he indicated that the wing shape, pattern, color and habit were more characteristic of species of *Proteoteras* Riley than of the coniferous feeding species that comprise the genus *Zeiraphera*. Our studies of the female genitalia show a relationship to the coniferous feeding species and support Heinrich's arrangement.

2. *Zeiraphera pacifica* Freeman

Zeiraphera pacifica Free. 1966, Can. Ent. 98: 588.

External characters. Frons with smooth, silver scales. Vertex light golden brown, roughly scaled. Antenna light grey with darker annulations; scape blackish brown inwardly, pale outwardly. Palpus whitish ochreous inwardly, blackish fuscous apically and outwardly. Thorax dark golden brown. Abdomen whitish grey. Fore- and mid-legs purplish black, with greyish bands. Hind leg purplish grey, with whitish bands. Forewing (Figs. 5, 6) with basal patch dark brown, whitish basally, narrowly margined with black apically, extending from just beyond basal fourth of costa obliquely outward to middle of wing, then at right angles inwardly to inner third of dorsum, costal region with

Fig. 1. *Z. claypoleana* ♂, Cincinnati, Ohio; Fig. 2. *Z. claypoleana* ♀, Cincinnati, Ohio; Fig. 3. *Z. canadensis* n. sp. ♀, Ottawa, Ontario; Fig. 4. *Z. canadensis* n. sp. ♀, McGillivray, B.C., *Picea engelmanni*; Fig. 5. *Z. pacifica* ♂, paratype, Sandspit, B.C., *Picea sitchensis*; Fig. 6. *Z. pacifica* ♀, paratype, Sandspit, B.C., *Picea sitchensis*; Fig. 7. *Z. improbana*, paratype of *pseudotsugana* (Kft.) Kaslo, B.C.; Fig. 8. *Z. improbana* ♀, Pagwal River, Ontario, larch; Fig. 9. *Z. improbana* ♀, Tabor, Ontario, *Larix laricina*; Fig. 10. *Z. improbana* ♀, Wawa, Ontario, *Larix laricina*; Fig. 11. *Z. improbana* ♀, Anarchist Mtn., B.C., *Larix occidentalis*; Fig. 12. *Z. fortunana* ♀ Paratype, Ottawa, Ontario, Fig. 13. *Z. fortunana* ♀, Black Sturgeon Lake, Ontario, *Picea glauca*; Fig. 14. *Z. fortunana* ♀, Yukon Territory, *Picea glauca*; Fig. 15. *Z. destitutana* ♀, Cape Breton, Nova Scotia; Fig. 16. *Z. destitutana* ♀, Black Sturgeon Lake, Ontario, *Picea glauca*; Fig. 17. *Z. destitutana* ♀, Black Sturgeon Lake, Ontario, *Picea glauca*; Fig. 18. *Z. destitutana* ♂, B.C., *Picea glauca*; Fig. 19. *Z. hesperiana* n. sp. ♂, Pavilion, B.C., *Pseudotsuga menziesii*; Fig. 20. *Z. hesperiana* n. sp. ♂, Kelowna, B.C., *Pseudotsuga menziesii*; Fig. 21. *Z. hesperiana* n. sp. ♀, William Head, B.C., *Pseudotsuga menziesii*; Fig. 22. *Z. hesperiana* n. sp. ♀, Yale, B.C., *Pseudotsuga menziesii*; Fig. 23. *Z. vancouverana* ♂, paratype, Ucluelet, Vancouver Island; Fig. 24. *Z. vancouverana* ♀, Vancouver Is., B.C., *Picea sitchensis*.



Male Genitalia: Fig. 25. *Z. claypolana*, Cincinnati, Ohio, Fig. 26. *Z. pacifica*, Sandspit, B.C., *Picea sitchensis*; Fig. 26a. *Z. pacifica*, Sandspit, B.C., *Picea sitchensis*; Fig. 27. *Z. ratzburgiana*, Germany; Fig. 28. *Z. canadensis*, n. sp. Ottawa, Ont.; Fig. 28a. *Z. canadensis*, n. sp. White Pt. Beach, Queens Co. N. S.; Fig. 28b. *Z. canadensis*, n. sp. Ottawa, Ont.; Fig. 28c. *Z. canadensis*, n. sp., Jacquet River, N. B.; Fig. 28d. *Z. canadensis*, n. sp., Zeballos R., B.C., *Picea* sp; Fig. 28e. *Z. canadensis*, n. sp., Zeballos R., B.C., *Picea* sp; Fig. 28f. *Z. canadensis*, n. sp., Prince Edward Island.

three blackish dashes; median band golden brown, the posterior half more distinct, narrowly edged with white and forming a dorsal patch; post median band dark brown; apical third irregularly mottled with golden, white and dark brown areas, the white area often appearing as a gradually broadening streak from tornus half way to costa; apical half of costa with evenly spaced, black dashes; fringe dark grey, with some white tipped scales, and with broken, darker basal line. Hind wing dark fuscous; fringe light grey, with a darker basal line.

Male Genitalia (Fig. 26). Uncus reduced, conical. Socii well developed, broadly sickle shaped. Tegumen broadly shouldered. Clasper well developed, long; heel broadly arcuate; apex broadly rounded. Aedeagus short, stout; apex truncate; cornuti a cluster of about sixteen elongate spines.

Female genitalia (Fig. 37). Apex of anterior and posterior apophyses somewhat broad. Ostial plate broad, not emarginate. Ostium small, somewhat cup shaped. Ductus bursae membranous, with slender sclerotized ring at neck of bursa. Two similar, conical signa present.

Flight period. Late June.

Type locality. Sandspit, Queen Charlotte Islands, British Columbia.

Distribution. Coastal British Columbia and Washington.

Host plant. *Picea sitchensis* (Bong.)

Remarks. This species is closely allied to the European *Z. ratzeburgiana* and to *Z. canadensis*. The head of *pacifica* is golden brown; that of *canadensis* is greyish. The dorsal patches of *canadensis* and *ratzeburgiana* are pale brown and triangular; those of *pacifica* are golden brown and rectangular.

3. *Zeiraphera canadensis* n. sp.

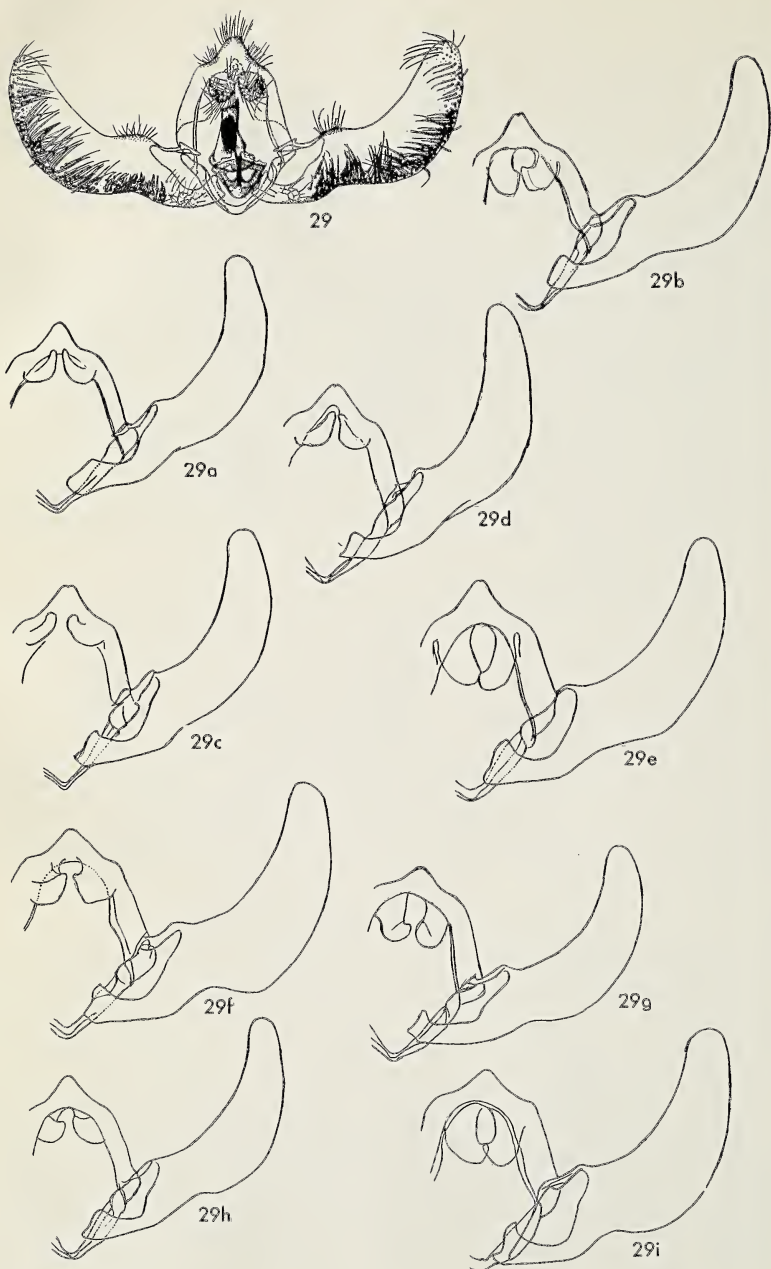
Steganoptycha ratzeburgiana: Fernald, 1884, *Rept. U. S. Dept. Agr.* p. 378; Packard, 1890, *Fifth Report U. S. Ent. Com.*, p. 845.

Epinotia ratzeburgiana: Fernald, 1903, in Dyar, *List N. Amer. Lep.*, No. 5233.

Enarmonia ratzeburgiana: Barnes and McDunnough, 1917, *Check List Lep. Bor. Amer.*, No. 7157.

Zeiraphera ratzeburgiana: Heinrich, 1923, *Bull.* 123, *U. S. Nat. Mus.*, p. 171; Forbes, 1923, *Cornell Univ. Agr. Exp. Sta. Mem.* 68, p. 446; Prentice, et al., 1965, *Dept. Forestry Can., Publ.* 1142, 4: 627.

External characters. Frons smoothly scaled, silvery. Vertex brown, roughly scaled. Antenna light brown, with black scales; scape with blackish scales inwardly, whitish fawn outwardly. Palpus whitish-ochreous inwardly, blackish fuscous anteriorly and outwardly. Thorax blackish brown, with a sprinkling of



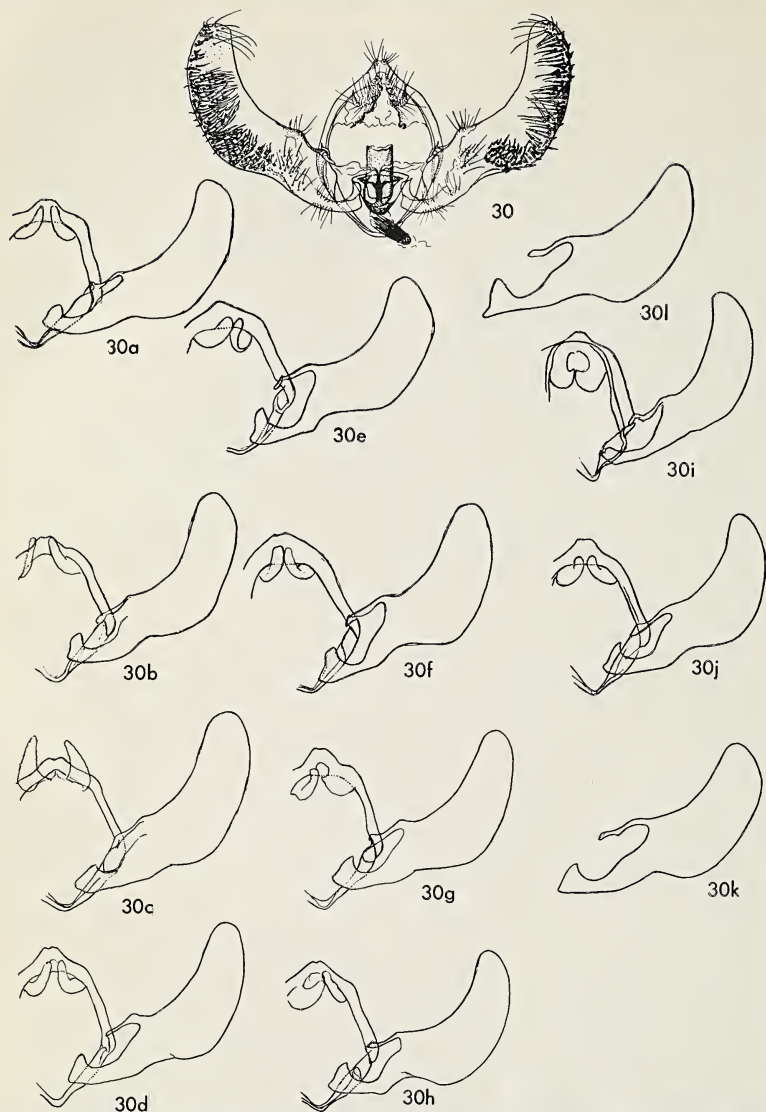
pale ochreous scales. Abdomen pale fuscous; terminal segment with pale brown scales. Fore- and mid-legs blackish fuscous, with pale brown bands. Hind tarsus pale fuscous, with pale brown bands. Forewing (Figs. 3, 4) with basal patch brown, mottled with brownish black, extending from just beyond basal fourth of costa vertically for a short distance, then obliquely angled outwardly to middle of wing, where it angles acutely inward to dorsum beyond basal third; costal area of basal patch with three or four small, blackish costal dashes; median band pale brown, divided into two large patches, one mottled with white scales on costal region, semi-circular, and containing a small costal dash, the other almost triangular with a broken, black, dorsal margin sometimes edged with white scales; post median band brown, becoming whitish on costal area where it contains a small costal dash; apical third irregularly mottled with whitish-grey, fuscous, and brown areas; near outer margin a brown, short, transverse band edged outwardly with white; fringe dark brown, with blackish areas and a broken, darker basal line. Hind wing dark fuscous; fringe light grey, with a darker basal line. Wingspread 12-15 mm.

Male genitalia (Figs. 28-28f). Uncus triangular. Socii broad. Tegumen broadly shouldered. Clasper well developed, long, constricted before apex; heel broadly extended and arcuate; sacculus slender. Aedeagus short, stout; cornuti a cluster of 9-18 spines.

Female genitalia (Figs. 38-38b). Apices of anterior and posterior apophyses somewhat widened. Ostial plate broad, not emarginate. Ostium small, cup-shaped. Ductus bursae membranous, with sclerotized slender ring near neck of bursa. One large and one small conical signum present.

Type material. Holotype male, Aylmer, Quebec, 13 June, 1960 (G. G. Lewis), reared from *Picea glauca*. Rearing no. 60-107. *Paratypes*: three males, three females, same locality and host as holotype 13-15 June, 1960. One male, Aylmer, Quebec, 2 July, 1935 (G. S. Walley). One male, Hull, Quebec, 26 June, 1946. F.I.S., reared from white spruce. Two males, Kingsmere (near Hull), Quebec, 14, 15 June, 1941. F.I.S., reared from white spruce. One male, Stittsville, Ontario, 25 June, 1948. F.I.S., reared from

Male Genitalia Fig. 29. *Z. improbana*, n. sp., Vermilion Bay, Ont., *Larix laricina*; Fig. 29a. *Z. improbana*, Laniel, Que., *Larix laricina*; Fig. 29b. *Z. improbana*, Hopedale, Labr; Fig. 29c. *Z. improbana*, Priceville, Ont., larch; Fig. 29d. *Z. improbana*, Burgessville, Ont., larch; Fig. 29e. *Z. improbana*, Ottawa, Ont.; Fig. 29f. *Z. improbana*, Aweme, Man.; Fig. 29g. *Z. improbana*, Beaver R., B.C., *Larix laricina*; Fig. 29h. *Z. improbana*, Nelson, B.C.; Fig. 29i. *Z. improbana*, Yorkton, N.J;



Male Genitalia: Fig. 30. *Z. fortunana*, paratype, Ottawa, Ont.; Fig. 30a. *Z. fortunana*, S. Milford, N.S.; Fig. 30b. *Z. fortunana*, Baddeck, N.S.; Fig. 30c. *Z. fortunana*, Bobcaygeon, Ont.; Fig. 30d. *Z. fortunana*, Black Sturgeon Lake, nt., *Picea glauca*; Fig. 30e. *Z. fortunana*, Black Sturgeon Lake, Ont., *Picea glauca*; Fig. 30f. *Z. fortunana*, Black Sturgeon Lake, Ont., *Picea glauca*; Fig. 30g. *Z. fortunana*, Black Sturgeon Lake, Ont., *Picea glauca*; Fig. 30h. *Z. fortunana*, Black Sturgeon Lake, Ont., *Picea glauca*; Fig. 30i. *Z. fortunana*, B.C., *Picea glauca*; Fig. 30j. *Z. fortunana*, B.C., *Picea glauca*; Fig. 30k. *Z. fortunana*, Dragon Lake, B.C., *Picea glauca*; Fig. 30l. *Z. fortunana*, Hospital Cr., B.C., *Picea engelmanni*.

white spruce. One male, three females, Hazeldean, Ontario, 2, 4 July, 1947. F.I.S., reared from white spruce. Three males, one female, South March, Ontario, 21-24 June, 1949. F.I.S., reared from white spruce. Four males, three females, Ottawa, Ontario, 27 June — 2 July, 1905 (C. H. Young). Two females, Ottawa, Ontario, 10, 12 July, 1906 (C. H. Young). One male, Ottawa, Ontario, 29 June, 1935 (C. H. Young). One female, Ottawa, Ontario, 28 June, 1931 (C. H. Young). Four females, Ottawa, Ontario, 26-29 June, 1948. F.I.S., reared from white spruce. One female, Ottawa, Ontario, 15 June, 1941. F.I.S., reared from white spruce. One female, Bell's Corners, Ontario, 11 June, 1941 (J. McDunnough), reared from spruce. All type specimens No. 9485 in the Canadian National Collection, Ottawa, Ontario.

Distribution. Transcontinental in Canada and the northern United States.

Host plants. *Picae glauca* (Moench) Voss and *P. sitchensis* (Bong.) Carr.

Remarks. This is the North American species that various authors have considered to be the European *Z. ratzeburgiana*. Our studies have shown that there are distinctive differences between them, mainly as follows:

Z. canadensis. Outer margin of basal patch distinctly concave or indented on costal half. Subapical white streak prominent, without white dashes through base of fringe. Female with one large and one small signum in bursa.

Z. ratzeburgiana. Outer margin of basal patch linear on costal half. Subapical white streak faint with prominent white dashes through base of fringe. Female with two equal sized signa in bursa.

4. *Zeiraphera improbana* (Walker)

Sciaphila improbana Wlk., 1863, *Cat. Lep. Het.* 28: 337.

Zeiraphera improbana (Wlk.), McDunnough, 1959, *Amer. Mus. Novit.* No. 1954: 2.

Sciaphila indivisana Wlk., 1863, *Cat. Lep. Het.* 28: 344. (New synonymy).

Paedisca diffinana Wlk., 1863, *Cat. Lep. Het.* 28: 378.

Zeiraphera diffinana (Wlk.), McDunnough, 1959, *Amer. Mus. Novit.* No. 1954: 2.

Cydia pseudotsugana Kft., 1904, *Can. Ent.* 36: 110. (New synonymy).

Thiodia pseudotsugana (Kft.), Dyar, 1904, *Proc. U. S. Nat. Mus.* 27: 927.

Epinotia pseudotsugana (Kft.), 1905, *Can. Ent.* 37: 89, 253.

Enarmonia pseudotsugana (Kft.), Barnes and McDunnough, 1917, *Check List Lep. Bor. Amer.* No. 7143.

Zeiraphera psuedotsugana (Kft.), Heinrich, 1923, *U. S. Nat. Mus. Bull.* 123: 171.

Zeiraphera pseudotsugana (Kft.), Klots, 1942, *Bull. Amer. Mus. Nat. Hist.* 79: 408.



Zeiraphera diniana: Heinrich, 1923, *U. S. Nat. Mus. Bull.* 123: 171, Fig. 287; Forbes, 1923, *Cornell Univ. Agt. Exp. Sta. Mem.* 68: 446; Prentice, et al., 1965, *Dept. Forestry Can., Publ.* 1142, 4: 629.

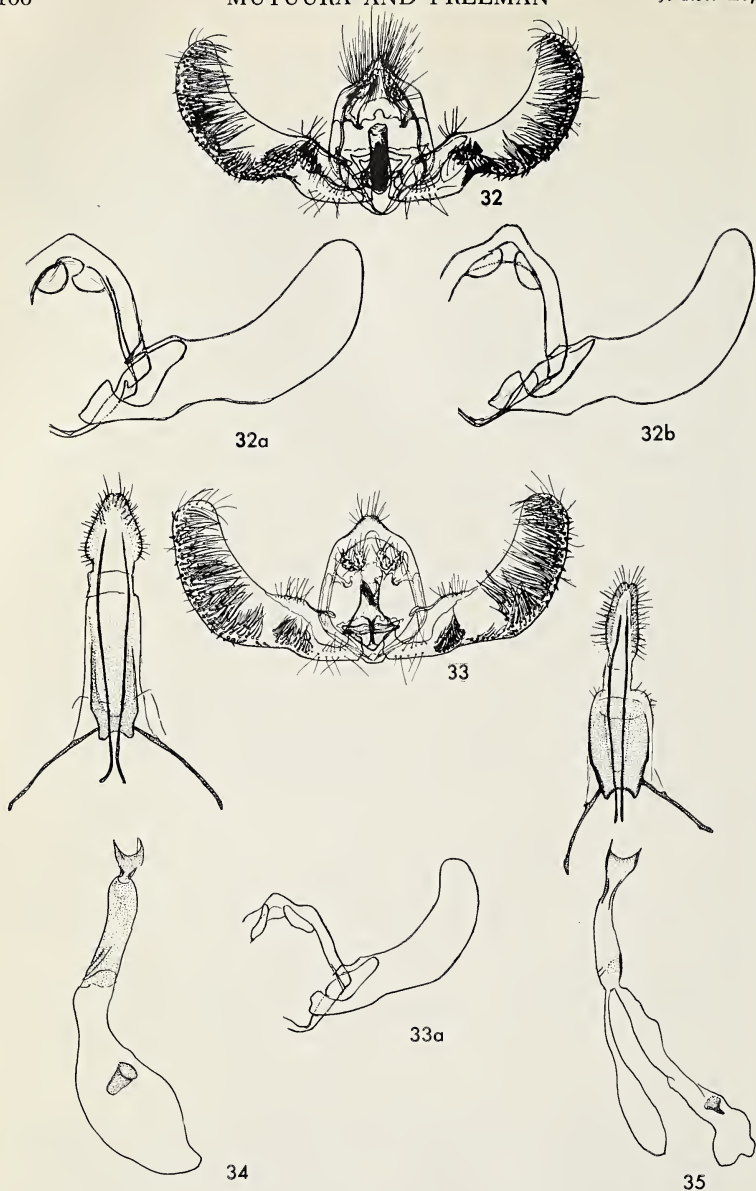
Zeiraphera sp. probably *diniana*: MacKay, 1959, *Can. Ent. Suppl.* 10: 97.

External characters. Frons roughly scaled, the scales greyish black, with pale fawn apices. Vertex rough, greyish black. Palpus fuscous inwardly, blackish outwardly. Antenna with alternate black and grey bands. Thorax blackish brown, the scales with pale fawn apices. Abdomen dark fuscous; terminal segment brownish. Tibiae and tarsi of fore- and mid-legs blackish fuscous, with pale fawn bands. Hind tibia and tarsus pale fuscous, with pale fawn bands. Forewing (Figs. 7-11) with basal patch, median band, and post median band variously obscured with a black or blackish grey ground color; basal patch extending obliquely outward from just beyond inner fourth of costa to middle of wing, then acutely angled inward to dorsum; median band greyish, divided into a small costal patch and a large dorsal patch, the costal patch semi-circular and containing two costal dashes, the brownish dorsal patch quadrate and edged with whitish-grey scales; post median band blackish with some brown scales; apical third blackish grey and with three costal geminations; submarginal line broken, black, with some golden brown scales; tornal spot greyish, obscure, and containing an irregular line of black and golden brown scales; fringe dark grey, whitish near tornus, and with broken black basal line. Hind wing dark grey; fringe fuscous, with dark grey basal line. Wingspread 10-18 mm..

Male genitalia (Figs. 29-29i). Uncus broadly conical; apex rounded, sometimes shallowly notched. Socii well developed, long, widest near middle. Aedeagus short, stout; apex truncate; cornuti a cluster of 30-60 elongate spines.

Female genitalia (Figs. 40-40c). Anterior and posterior apophyses longer than in other species with one signum. Ostial plate

Male Genitalia Fig. 31. *Z. destitutana*, Black Sturgeon Lake, Ont., *Picea glauca*; Fig. 31a. *Z. destitutana*, Parrsboro, N.S.; Fig. 31b. *Z. destitutana*, Baddeck, N.S.; Fig. 31c. *Z. destitutana*, Edmundston, N.B., *Abies balsamea*; Fig. 31d. *Z. destitutana*, Mt. Lyall, Que; Fig. 31e. *Z. destitutana*, Upsala, Ont., *Picea glauca*; Fig. 31f. *Z. destitutana*, Finland, Ont., *Picea glauca*; Fig. 31g. *Z. destitutana*, Black Sturgeon Lake, Ont. *Picea glauca*; Fig. 31h. *Z. destitutana*, S. E. Corner, Yukon T., *Picea glauca*; Fig. 31i. *Z. destitutana*, Kamloops, B.C., *Picea engelmanni*; Fig. 31j. *Z. destitutana*, Big Bend Hwy., B.C., *Picea engelmanni*; Fig. 31k. *Z. destitutana*, Big Bend Hwy., B.C., *Picea engelmanni*; Fig. 31l. *Z. destitutana*, Scully Ck., B.C., *Picea sitchensis*; Fig. 31m. *Z. destitutana*, Nation River, B.C., *Abies laciocarpa*.



Male Genitalia Fig. 32. *Z. hesperiana* n. sp., Pavilion, B.C., *Pseudotsuga menziesii*; Fig. 32a. *Z. hesperiana* n. sp., Canal Flats, B.C., *Pseudotsuga menziesii*; Fig. 33. *Z. vancouverana*, paratype, Ucluelet, Vancouver Is., B.C.; Fig. 33a. *Z. vancouverana*, paratype, Ucluelet, Vancouver Is., B.C.
 Fig. 34-42. Female genitalia; Fig. 34. *Z. hesperiana* n. sp. Powell River, B.C., *Pseudotsuga menziesii*; Fig. 35. *Z. vancouverana*, Vancouver Is., B.C.

narrow, emarginate. Ostium small, cup shaped. Ductus bursae slightly sclerotized, without sclerotized ring at neck of bursa. One signum present, variable in size and shape.

Flight period. Late June to early August.

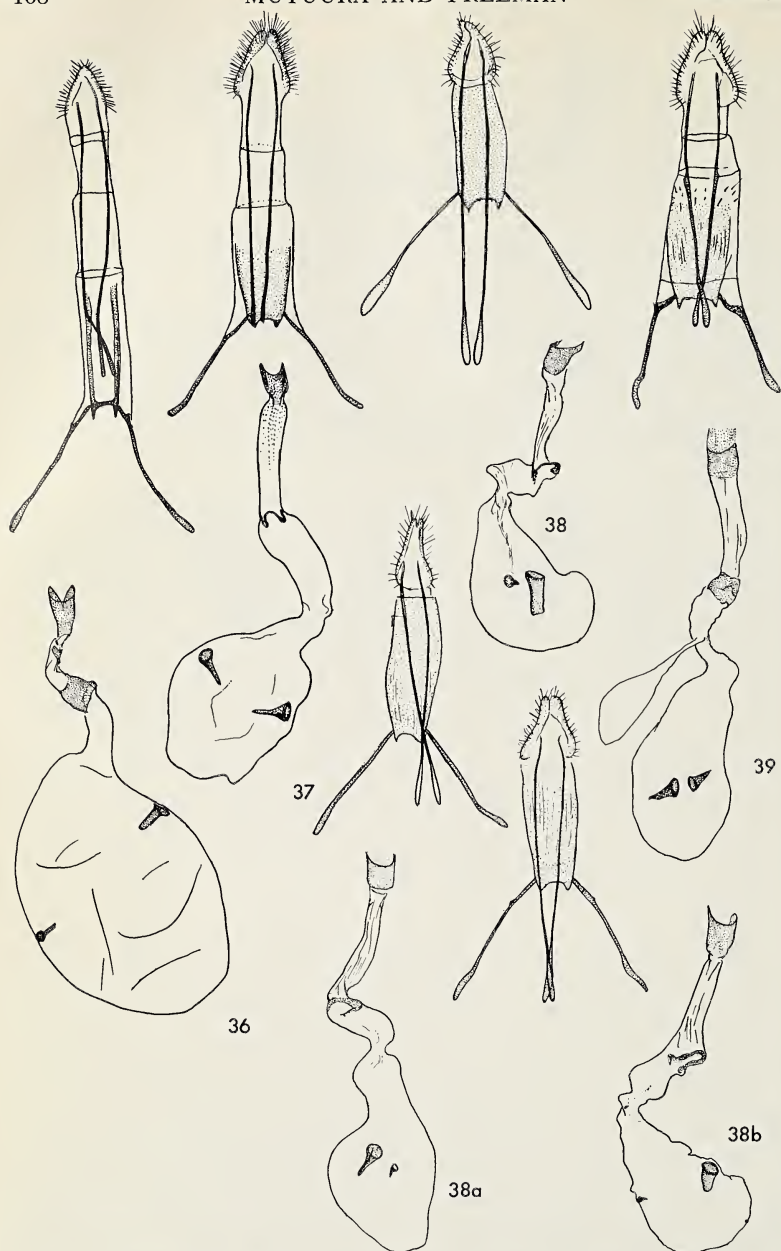
Type locality. St. Martin's Falls, Albany River, Northern Ontario.

Distribution. Transcontinental in southern Canada and the northern United States.

Host plants. *Larix laricina* (Du Roi) K. Koch and *L. occidentalis* Nutt.

Remarks. This is the species that North American authors have usually associated with the name *Z. diniana* Gn. as previously noted in the introduction to this paper. The names *improbana* Wlk., and *diffiniana* Wlk. have been associated with various species during their taxonomic history. McDunnough (1959) with the help of lepidopterists at the British Museum (Natural History), London, England, established that the two Walker names were synonymous and applied to a *Zeiraphera* species. Subsequently Obraztsov (in litt.) studied Walker's type of *indivisana* and realized that it also was synonymous with *improbana*. All three were described from St. Martin's Falls, are variants of a single species, and are indistinguishable from the North American larch feeding species.

Kearfott (1904) described *pseudotsugana* from flown specimens taken by Dyar at Kaslo, Kokanee Mt., and iKtchener Glacier, British Columbia. Dyar also reared specimens from *Pseudotsuga* which he thought were the same species. The paratype at the American Museum of Natural History, New York City, N.Y., is a headless female from Kaslo (Fig. 7) and is undoubtedly the dark colored *Larix* feeder. The only other type material in existence is a paratype in the Canadian National Collection, Ottawa, Ont., from Kitchener Glacier. It also is the *Larix* feeder. Both of these paratypes agree with the original description and it is apparent that Kearfott did not have specimens reared from *Pseudotsuga*. It follows therefore, that the oldest name *improbana* applies to this species. It may be recognized by the dark, indistinct maculation and its host preference of *Larix*.



Female genitalia: Fig. 36. *Z. claypoleana*, Cincinnati, Ohio; Fig. 37. *Z. pacifica*, paratype, Sandspit, B.C., *Picea sitchensis* Fig. 38. *Z. canadensis*, n. sp., Bell's Corner, Ont., spruce; Fig. 38a. *Z. canadensis*, n. sp., Radium Hot Springs, B.C., *Picea* sp; Fig. 38b. *Z. canadensis*, n. sp., Hazelton, B.C., *Picea sitchensis*; Fig. 39. *Z. ratzburgiana*, Germany, *Picea excelsa*.

5. *Zeiraphera fortunana* (Kearfott)

Epinotia fortunana Kearfott, 1907, *Can. Ent.* 39:126.

Enarmonia fortunana (Kft.), 1917, Barnes and McDunnough, *Check List Lep. Bor. Amer.*, No. 7168.

Zeiraphera fortunana (Kft.), Heinrich, 1923, *U. S. Nat. Mus. Bull.* 123: 172, fig. 288; Forbes, 1923, *Cornell Univ. Agric. Exp. Sta. Memoir* 68:446; Klots, 1942, *Bull. Amer. Mus. Nat. Hist.* 79: 402; MacKay, 1959, *Can. Ent. Suppl.* 10: 96, fig. 85; Prentice, et. al., 1965, *Dept. Forestry Can.*, Publ. 1142, 4: 630.

External characters. Frons smoothly scaled, whitish grey. Vertex with long, whitish-grey scales. Palpus cream white, blackish outwardly. Antenna pale fawn. Thorax dark brown, edged with pale fawn. Abdomen dark fuscous. Tibiae and tarsi of fore- and mid-legs blackish fuscous, with whitish-grey bands. Hind tibia and tarsus pale fuscous, with whitish-grey bands. Forewing (Figs. 12-14) with basal patch cream-white, mottled with blackish, and extending from beyond inner fourth of costa obliquely outward to middle of wing, then obtusely angled inward to dorsum, which it reaches just beyond inner third; median band creamy-white, angulated at middle of wing, and containing a shining, pale ochreous line and a blackish costal dash; post-median band blackish brown, irregular in outline, broader at trailing edge; apical third of wing irregularly mottled with whitish-brown and blackish-brown areas, with three costal dashes, and a broken submarginal line; fringe fuscous, with broken darker basal line. Hind wing fuscous; fringe pale fuscous, with fuscous basal line. Wingspread 12-15 mm.

Male genitalia (Figs. 30-30l). Uncus reduced, with apex truncate or slightly notched. Socii well developed, broadly sickle shaped. Tegumen not produced at the shoulder. Clasper short; apex narrow. Aedeagus short, stout; apex truncate; cornuti a cluster of 16-24 elongate spines.

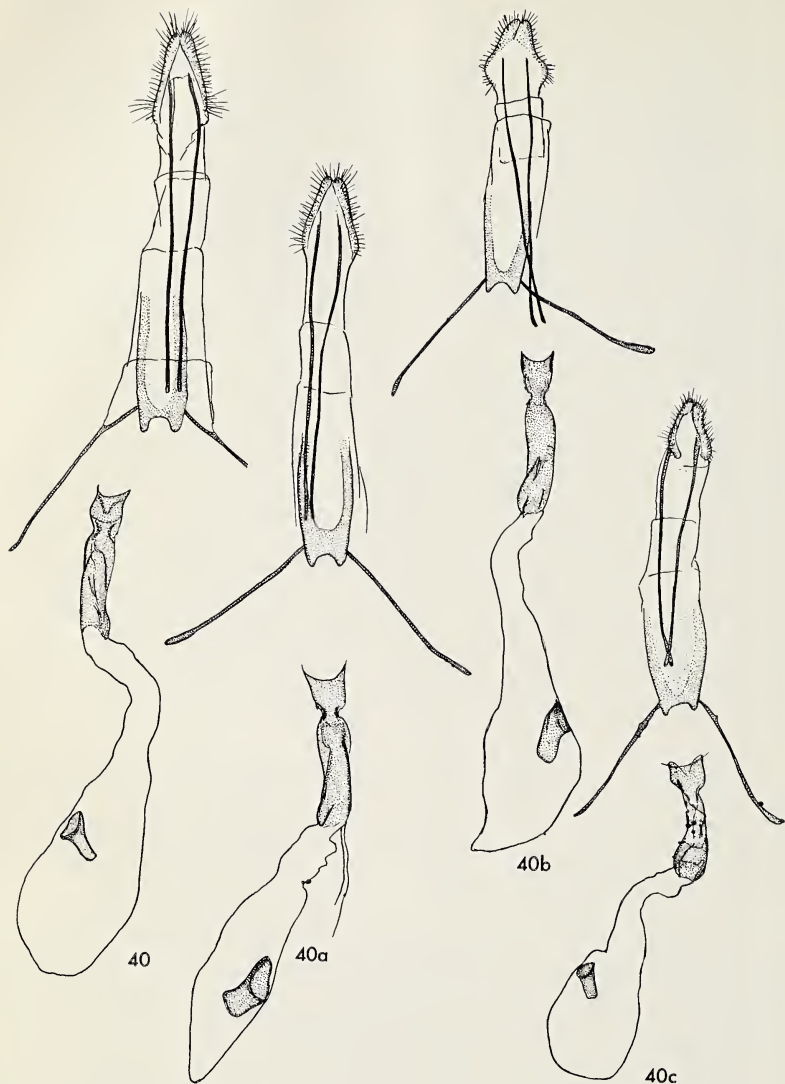
Female genitalia (Figs. 41-41c). Anterior and posterior apophyses moderate in size. Ostial plate broad, emarginate. Ostium somewhat cup shaped. Ductus bursae weakly sclerotized. One signum present, somewhat conical, rather large.

Flight period. Early June to late July.

Type locality. Ottawa, Ontario.

Distribution. Nova Scotia to British Columbia.

Host plants. *Picea glauca* (Moench) Voss, *P. engelmanni* Parry.



Female genitalia: Fig. 40. *Z. improbana*, Hopedale, Labr., Que.; Fig. 40a. *Z. improbana*, Ottawa, Ontario; Fig. 40b. *Z. improbana*, Anarchist Mtn., B.C., *Larix occidentalis*; Fig. 40c. *Z. improbana*, Anarchist Mtn., B.C., *Larix occidentalis*.

Remarks. This species apparently is well distributed throughout the spruce regions of Canada. It is closely allied to *Z. destitutana* but *fortunana* is smaller in wingspread and in size of genitalia. The frons and vertex of *fortunana* are whitish ochreous; those of *destitutana* are greyish brown. The uncus of *fortunana* is somewhat notched; that of *destitutana* is rounded at the apex. The ostial plate of *fortunana* is broader and shorter than that of *destitutana*.

6. *Zeiraphera destitutana* (Walker)

Sciaphila destitutana Wlk., 1863, *Cat. Lep. Het.* 28: 339.

Zeiraphera destitutana (Wlk.), McDunnough, 1959, *Amer. Mus. Novit.* No. 1954: 3.

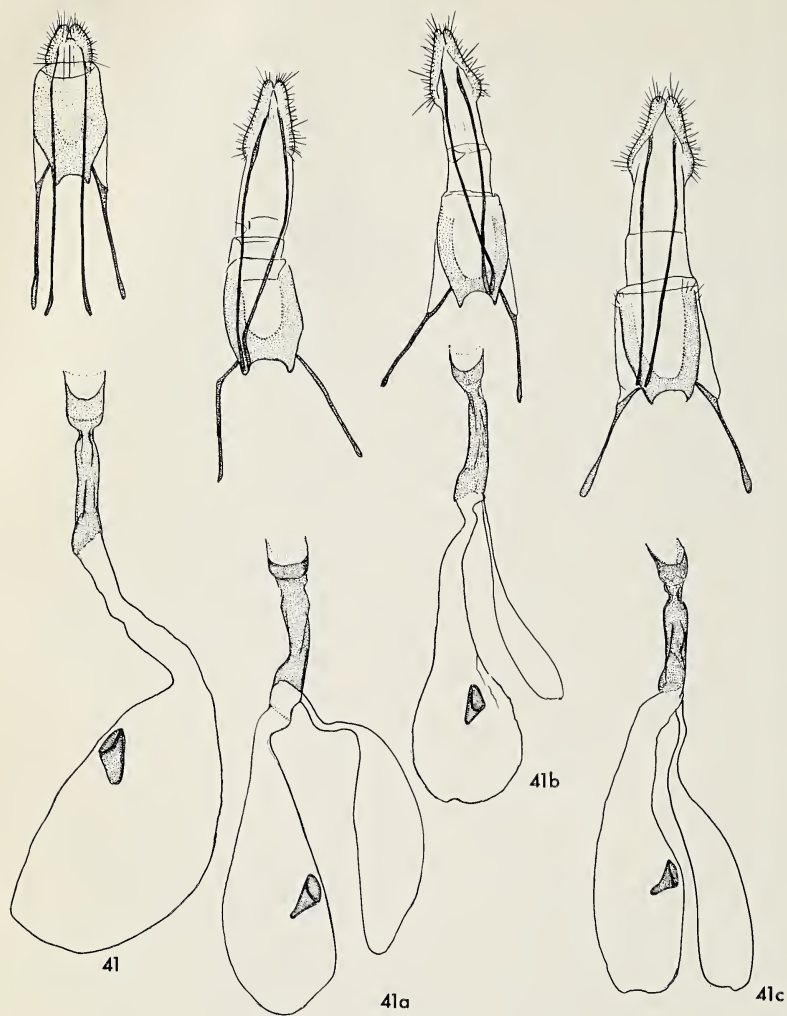
External characters. Frons smooth, white below, with overlapping, long, greyish-brown scales laterally and dorsally. Vertex greyish brown. Palpus whitish grey inwardly, dark fuscous outwardly and apically. Antenna fuscous, with darker fuscous scales; scape blackish fuscous inwardly, much paler outwardly. Thorax brownish fuscous. Abdomen pale fuscous. Tibiae and tarsi of fore- and mid-legs blackish fuscous, with greyish bands. Hind leg whitish. Forewing (Figs. 15-18) with basal patch whitish grey, mottled with blackish, margined outwardly with black, costal margin with three black costal dashes; basal patch extending from beyond basal fourth of costa obliquely outward to middle of wing, then almost at right angles inwardly to dorsum, which it reaches just beyond basal half; median band whitish, constricted at middle of wing to form a costal spot and a dorsal patch; an irregular blackish post median band extending across the wing; apical third irregularly mottled with black, white, whitish-grey, and brownish scales; costa with three blackish geminations on apical third; subapical spot black, confluent with the two outer costal geminations; tornal region whitish; subapical line broken into black spots; fringe with blackish and brownish scales, whitish near tornus and with a black and white basal line. Hind wing blackish fuscous; fringe blackish fuscous, with black basal line. The female is more distinctly marked with white than the male. Wingspread 14-17 mm.

Male genitalia (Figs. 31-31m). Uncus poorly developed. Tegumen not strongly shouldered. Clasper broad, broadly rounded apically. Cornuti a cluster of about 24-40 elongate spines.

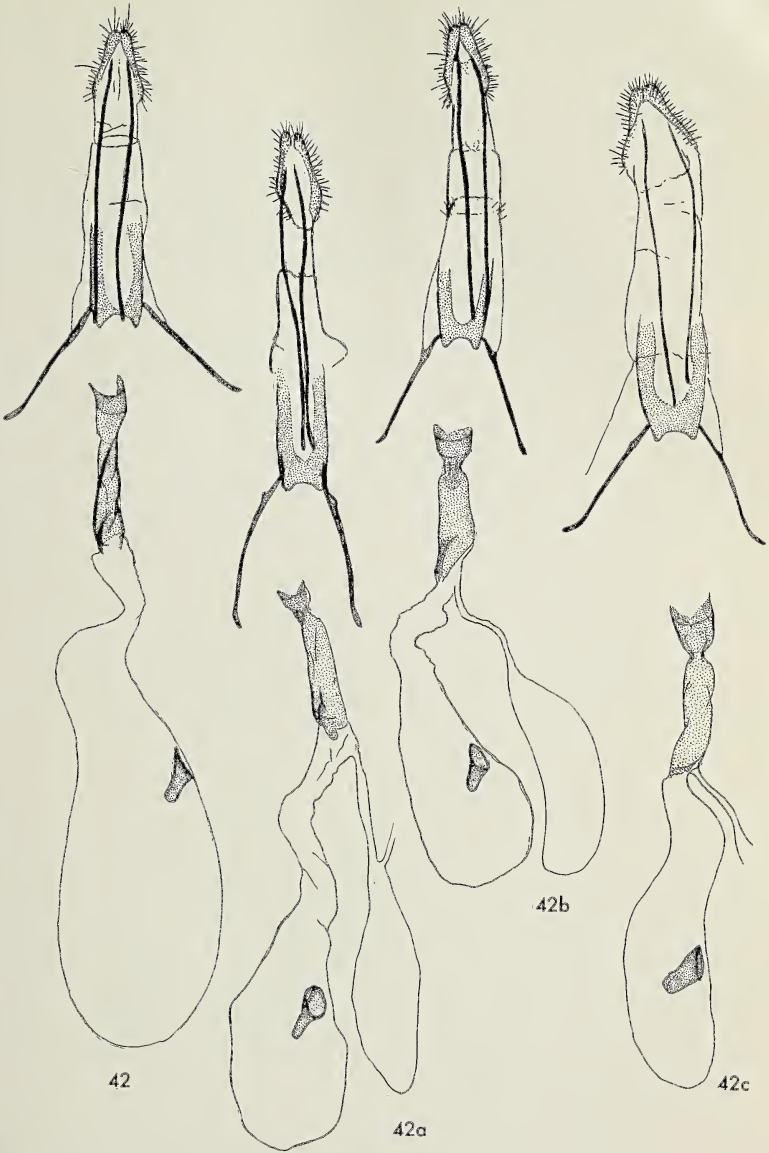
Female genitalia (Figs. 42-42c). Similar to those of *Z. improbana* Wlk.

Flight period. July and early August.

Type locality. St. Martin's Falls, Albany River, Ontario.



Female genitalia: Fig. 41. *Z. fortunana*, paratype, Ottawa, Ont.; Fig. 41a. *Z. fortunana*, Black Sturgeon Lake Ont., *Picea glauca*; Fig. 41b. *Z. fortunana*, Black Sturgeon Lake, Ont., *Picea glauca*; Fig. 41c. *Z. fortunana*, Yukon Territory, *Picea glauca*; Fig. 42a. *Z. destitutana*, Black Sturgeon Lake, Ont., *Picea glauca*; Fig. 42b. *Z. destitutana*, Nelson, B. C., *Picea glauca*; Fig. 42c. *Z. destitutana*, Hudson-Hope, B.C., *Picea glauca*.



Distribution. Nova Scotia to British Columbia.

Host plants. *Picea glauca* (Moench) Voss, *P. mariana* (Mill.) B.S.P., *P. engelmanni* Parry, *P. sitchensis* (Bong.) Carr., *Abies balsamea* (L.) Mill., *A. lasiocarpa* (Hook.) Nutt. and *A. amabilis* (Dougl.) Forb.

Remarks. This species has been confused with *Z. fortunana* (Kft.). However, it is larger, and the forewing has a mottled appearance and a larger dorsal patch. It also has considerable variation from light contrasting markings to dark suffused ones. The apex of the male uncus is entire, not notched as in *fortunana*, and the female ostial plate of *distitutana* is longer and narrower, resembling that of *improbana*.

7. *Zeiraphera hesperiana* n. sp.

External characters. Frons roughly scaled, dark fuscous. Vertex greyish brown, roughly scaled, with a large tuft of the scales between antenna and upper side of compound eye. Palpus whitish ochreous inwardly, darker apically and outwardly. Antenna fawn with whitish scales; inner side of scape blackish, outer side whitish. Thorax dark brown, sprinkled with pale scales. Abdomen pale fuscous. Tibiae and tarsi of fore- and mid-legs blackish fuscous, with greyish bands. Hind tibia pale fuscous; tarsus somewhat blackish fuscous with a greyish band at apex. Forewing (Figs. 19-22) with basal patch grey, mottled with black spots, and extending from just beyond inner fourth of costa obliquely outward to middle of wing, then acutely angled inwardly to just beyond inner third of dorsum; median band divided into a whitish grey costal area and a large, whitish, semi-circular patch on dorsum, the costal area usually with three blackish costal dashes, the dorsal patch extending from dorsum to middle of wing, with four obscure black dashes on dorsal edge, and with mottled black and light brown scales in the middle; post-median band irregular, blackish, extending across the wing, narrower at costa; apical third with four blackish costal geminations, and a black subapical spot; tornal spot golden brown or whitish, mottled with black; submarginal line broken, black and brown; fringe dark grey, with some white-tipped scales, and a broken, darker, basal line. Hind wing dark fuscous; fringe light grey, with a darker basal line. Wingspread 15.0-20.5 mm.

Male genitalia (Figs. 32-32b). Uncus reduced; apex rounded. Socii well developed, broadly sickle shaped. Tegumen rounded at shoulder. Clasper large, long; apical region broad. Aedeagus short, stout; apex truncate; cornuti a cluster of about 23-34 elongate spines.

Female genitalia (Figs. 34). Ostial plate narrow, emarginate. Ostium small, cup-shaped. Ductus bursae slightly sclerotized, with a broad, sclerotized ring at neck of bursa. One sub-conical, rather large signum present.

Type material. Holotype male, Courtenay, B.C., 9 July, 1951, F.I.S., reared from Douglas fir. *Paratypes*: Two males, two females, Cowichan Lake, 27 July, 1944 (M. L. Prebble). Two males, Bridesville (Osoyoos district), 17 July, 1952. One male, Kaleden (Similkameen district), 8 July, 1952. One male, one female, Eneas Creek (Okanagan district) 6, 5 July, 1954. One male, Kitchener, 20 July, 1950. One male, Shuswap Falls (Kamloops district), 24 July, 1951. One male, Tappen Valley (Kamloops district), 17 July, 1954. One male, Thupana Inlet (Vancouver Island) 28 July, 1954. One female, Powell River (New Westminster district), 24 July, 1950. One male Canal Flats, 25 July, 1950. One female, Dutch Creek (Kootenay district), 26 July, 1949. One female, Fairmont Hot Springs (Kootenay district), 27 July, 1949. All the above paratypes are from British Columbia and reared from Douglas fir by the Canada Forest Insect Survey. All type specimens No. 9486 in the Canadian National Collection, Ottawa, Ontario.

Distribution. Southern British Columbia.

Host plant. *Pseudotsuga menziesii* (Mirble) Franco.

Remarks. On the basis of similarities in the genitalia, this species is closely allied to *Z. destitutana*.

8. *Zeiraphera vancouverana* McDunnough

Zeiraphera vancouverana McDunnough, 1925, *Can. Ent.* 57: 21.

External characters. Frons and vertex roughly scaled, dark brown. Antenna blackish brown; scape blackish brown inwardly, pale brown outwardly. Palpus pale fuscous inwardly, dark brown outwardly. Thorax and tegula dark brown. Abdomen blackish brown; terminal segment paler. Fore- and mid-legs blackish brown, with pale whitish-brown bands. Hind leg pale whitish fuscous; tarsus somewhat fuscous, with pale whitish bands. Forewing (Figs. 23, 24) with basal patch fuscous, mottled with brown, margined outwardly with blackish on dorsal half, and extending from beyond inner fourth of costa obliquely outward to middle of wing, then acutely angled inwardly to dorsum just beyond inner third; median band divided into a pale brown costal portion and a whitish grey, sub-rectangular, oblique dorsal

patch; apical third mottled with whitish grey, brown, and dark fuscous areas; fringe dark brown, with a broken blackish-fuscous basal line. Hind wing dark brown; fringe paler, with a pale blackish-fuscous basal line. Wingspread 11-14 mm.

Male genitalia (Figs. 33, 33a). Resembling those of *fortunana*. Uncus round at apex, not notched. Socii well developed, broadly sickle shaped. Tegumen angled at the shoulder. Apical region of clasper only slightly narrowed. Aedeagus short, stout; apex truncate; cornuti a cluster of 3-6 elongate spines.

Female genitalia (Fig. 35). Anterior and posterior apophyses short. Ostial plate short and broad, narrower basally. Ostium cup-shaped. Ductus bursae slender, not sclerotized. One small signum present.

Flight period. July.

Type locality. Ucluelet, Vancouver Island, British Columbia.

Distribution. Known only from Vancouver Island, British Columbia.

Host plants. *Picea sitchensis* (Bong.) Carr. and *P. engelmanni* Parry.

Remarks. On the basis of the male genitalia, this species is closely allied to *Z. fortunana* (Kft.). It is the smallest species in the genus.

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NOTES ON EACLES PENELOPE (SATURNIIDAE)

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THE LARVA OF THE NEOTROPICAL MOTH *Eacles penelope* (Cramer) has been figured and described previously, (Burmeister, 1879). Packard (1905) gives a copy of Burmeister's plate. The coloring of the figure of the larva appears very dim and faded when compared against the living specimens which have very bright and vivid coloring. According to Packard it lives on Melastomeae and Guava (*Psidium pomiferum*) one of the Myrtaceae. As the result of being sent eggs of this species, I have been able to rear it, and make some further observations on its habits and life-history.

On 30. IX. 1963 about 400 ova were received from Sr. Fritz Plaumann of Nova Teutonia, Santa Catarina, Brazil. Although these had been sent by air-mail they had been in transit for over two weeks; most had hatched *en route*; the few survivors appeared rather weak. They were at once put into a small glass-topped metal tin of 3 inches diameter, containing a wet filter paper to maintain them at a high humidity. They were offered a choice of Laburnum (*Laburnum anagyroides*), Privet (*Ligustrum ovalifolium*), Walnut (*Juglans regia*), and Beech (*Fagus sylvatica*). All these leaves were nibbled, but the larvae finally settled on Beech. They were maintained on this until the end of the penultimate instar, when the supply failed. Evergreen oak (*Quercus ilex*) was offered and accepted throughout the final instar. Privet which was also offered was firmly refused. When fully grown the larvae left the food and started wandering. They were then removed to a large tin containing moist peat and they burrowed into this to form a pupa in a pressed out cell some nine inches down. Of about fifty larvae that were still alive on receipt, about fifteen actually started to feed, one or two died at each moult and only 3 pupae were obtained. It is con-

sidered that the larvae which failed to start feeding did so because they were already weak from starvation rather than the possible unsuitability of the food. The larvae were reared at 20-25°C and were subjected to British daylight conditions from September thro December, but had erratic artificial light during the evening while the stock was being attended to. Under these conditions the pupae entered diapause and the moths did not eclose for six months.

The duration in days of the six instars is given below. To obtain the figure for the final instar an estimate of 6 days between entering the soil and pupation has been allowed. This is a figure compatible with my experience of other underground pupating species that do not hibernate (or diapause) as pre-pupae.

1st — 11; 2nd — 10; 3rd — 10; 4th — 8; 5th — 15; 6th — 31.

Total — 85. Pupal duration 24 weeks.

A total life-cycle of 9 months is clearly incompatible with normal feral conditions. Other species bred contemporaneously, such as *Dirphiopsis eumedide* (Stoll) and *Automeris beckeri* (Herrich-Schäffer) proved to have a six-month life-cycle. No explanation can be offered for this, it being one of the few Neotropical species bred in England that has had an unusual life-cycle period. It may well be that this species has a facultative light-controlled diapause and is much more critical concerning its requirements than are the species of various other Neotropical genera. One has only to study the enormous range of latitude over which both this species and *E. imperialis* (Druce) range (Packard, 1905; Draudt, 1930) to realise that they must have varying diapause requirements in differing parts of their range. From the Atlantic States *imperialis* has a pupal period of nine or ten months (Crotch, 1956) whereas from Panama, bred contemporary with *penelope*, the pupal period was two months.

THE OVA — Like other Citheroninae, very large; in form, elliptical, with a marked central, angular, ridge, flat on base, indented inwards on top. Maximum diameter 3.9 mm; minimum, 3.2 mm; height 2.0 mm. The larvae being mainly hatched on arrival, the color was not observed, but in those unhatched, the larvae were clearly visible, curled up around the equatorial plane, thro the translucent golden colored shells.

THE LARVA — Due to pressure of other work it was not possible to keep accurate details of all the larval stages. Fig. 1, however gives a better idea of the fullgrown larva than can any description. Although only a few larvae were available it was noted that they appeared to prefer a solitary life.



Fig. 1. Full-grown larva of *Eacles penelope*.

Fig. 2. Adult *Eacles penelope*; Top ♀, Lower ♂.

THE IMAGO — The three obtained all eclosed about one hour after sunset, but did not become active in their cage until the following night. This is perhaps not surprising since during June in England there is only 2-3 hours of darkness — considerably less than would normally be experienced in Brazil. It is worth mentioning in this connection that *E. imperialis*, with ten hours of darkness, emerged at dusk and was paired within six hours.

Particularly striking was the very pungent and all-pervading odor of the meconium from the newly emerged moth. To the author it resembled the odor of onions which have just started to go rotten and have been kept in a closed container for some days. It closely resembled, but was subtly different from, the odor given off by the meconium of *Periphobia hircia* (Cramer), but was not so persistent. The latter genus has previously been commented on by Blest (1960a), but the odor from *E. penelope* does not appear to have been recorded. The adults show a specialised procryptic coloration when at rest (Blest, 1960b) and it may be that the obnoxious odor serves as protection during the dangerous period while the wings are expanding and hardening. When disturbed shortly after this, the moths flicked themselves rapidly about the floor, from right way up to upside down, finally coming to rest with legs and antennae tightly tucked to body.

ACKNOWLEDGEMENTS

I should like to thank Dr. David Blest both for helpful criticism and for taking the photograph illustrating the larva, and Simon Frey of the Virus Research Unit for that illustrating the adults. The cost of obtaining the eggs was supported by the United States National Institutes of Health, Project No. GM-07109.

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REMARKS ON
THE GENUS *ZERA* EVANS IN MEXICO

WITH A NEW RECORD

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FOUR SPECIES OF *ZERA* have been previously recorded from Mexico, and in most cases the data was very incomplete. Hoffmann lists three species from that country: *scybis* (Godman & Salvin), which is a synonym of *noelckeni* (Mabille); *pelopea* (Godman & Salvin), which is a synonym of *tetrastigma* (Sepp); and *hyacinthinus* (Mabille), which he said he had not seen in Mexico. Evans lists three species contained in the British Museum from Mexico: *noelckeni*, *hyacinthinus*, and *eboneus* (Bell). During the process of making a careful study of the HesperIIDae of Mexico I have found that there are actually five species of *Zera* in Mexico, one of which I am recording for the first time.

***Zera noelckeni* (Mabille) 1891**

Synonym.—*scybis* Godman & Salvin 1894: Atoyac, Veracruz, Mexico.

Type locality.—Bogota.

General distribution.—Mexico, Panama, Colombia, Venezuela, Ecuador (Loja, Ambato), Peru (Cuzco, Chanchamayo, Huanca-bamba), and Bolivia (Cochabamba, Tanampaya, San Jacinthe).

Mexican distribution.—Atoyac, Veracruz; Sierra Madre del Sur; Cuenca del Rio Balsas; and Colima.

Remarks.—This species was first recorded from Mexico by Godman & Salvin as *scybis* based on a specimen from Atoyac, Veracruz. Hoffmann listed several locations which are mentioned above. In the large number of specimens of HesperIIDae that Dr. Tarsicio Escalante, Mexico, D. F. sent me for determination there were no examples of this species. During the eighteen trips that I have made to Mexico I have not as yet turned up this species. From the available data *noelckeni* is apparently rare in Mexico as well as in some of the Central American areas.

¹I would like to express my thanks to the National Science Foundation for Research Grant GB-4122 which is making this study of the HesperIIDae of Mexico possible.

Zera hosta Evans 1953

Type locality. — Costa Rica.

General distribution. — Mexico, Costa Rica, and Colombia.

Mexican distribution. — Sta. Rosa, Comitan, Chiapas, 1 male May 1965.

Remarks. — Evans described *hosta* as a subspecies of *phila* (Godman & Salvin) based on the general difference of the secondaries on the lower surface, *hosta* being bluish-white over the discal one half to two thirds of the wing, and *phila* being entirely tawny, with some black spots. The general range of the two overlaps thus bringing up the question as to whether they are separate subspecies or species. For the present I will consider them to be specifically distinct.

New record for Mexico. — the above mentioned male, which was obtained from Dr. Escalante, is the first record of this species from Mexico.

Zera hyacinthinus (Mabille) 1877

Type locality. — ?

General distribution. — Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, and Colombia.

Mexican distribution. — Presidio, Veracruz, 1 male, August 1951 (A. Ramirez); Ajijic, Jalisco, 1 male, 27 September 1965, and 1 male, 5 October 1965 (Robert Wind); and 2 males and 1 female, Oaxaca, Oaxaca, 22 June 1966 (H. A. Freeman).

Remarks. — Considerable confusion has centered around this species for many years. Godman & Salvin figured the male and genitalia of *tetrastigma* as *hyacinthinus*. Hoffmann stated that he had not seen any examples from Mexico indicating that possibly he was not familiar with the exact status of the species. Evans recorded four males and three females from Mexico with no other data. I have in my collection the above mentioned specimens listed under Mexican distribution of this species from Mexico. From the available data indications are that this species of *Zera* is the predominant one in Mexico.

Zera tetrastigma (Sepp) 1848

Synonyms. — *menedemus* Godman & Salvin 1894: Panama; *pelozea* Godman & Salvin 1894: Amazons.

Type locality. — Surinam.

General distribution. — Mexico, Guatemala, Nicaragua, Panama, Colombia, Trinidad, British Guiana, French Guiana, Peru (Chanchamayo, Chaquimayo), Bolivia (Buenavista), Upper Amazons (Iquitos, Tonantins, S. Paulo de Olivenca), and Para.

Mexican distribution. — Sierra Madre Occidental (Nayarit);

Catemaco, Veracruz, one male, November 1964, and one female, January 1952 (A. Ramirez). Specimens obtained from Dr. Escalante.

Remarks. — The considerable variation of this species has resulted in two synonyms: *menedemus*, having the secondaries below with the dorsal half white; and *pelopea*, having the secondaries below entirely dark brown, with bands absent or vestigial. Typical *tetrastigma* is dark brown on the secondaries below with well-marked black central and submarginal bands, and some bluish-white over the dorsal half of the wing.

Zera eboneus (Bell) 1947

Type locality. — Ojo de Agua, Veracruz, Mexico.

General distribution. — Mexico.

Mexican distribution. — Ojo de Agua, Veracruz, 12 June 1941.

Remarks. — From Bell's original description and genitalia figure *eboneus* is apparently a distinct species. Evans states that the genitalia are similar to those of *belti* (Godman & Salvin), and that *eboneus* is probably an aberration or subspecies of *belti*. However as he never examined the type it seems most unlikely that the two are the same species since they are so different superficially.

Key to the Mexican species of *Zera*

- 1a. Primaries above with dark central area2
- 1b. Primaries above plain black5
- 2a. Primaries above with dark central area extending to base and lower end of cell; three apical spots3
- 2b. Primaries above with dark central area not extending to base, which is broadly violaceous, nor to end of cell; 1-3 apical spots4
- 3a. Primaries above with dark bar at end of cell; secondaries below with dorsal half bluish-white, but tawny colouring from costa runs narrowly along outer margin to vein 1b*nolckeni* (Mab.)
- 3b. Primaries above with no dark bar at end of cell; secondaries below with dorsal one half to two thirds bluish-white*hosta* Evans
- 4a. Primaries with tornus truncate and dorsum slightly concave; primaries below with tornal area broadly tawny, often reaching the costa and unmarked except for an inconspicuous discal spot; usually 3 apical spots*hyacinthinus* (Mab.)
- 4b. Primaries not truncate at tornus and dorsum more or less straight; primaries below with tornal tawny area restricted and marked with a large dark central spot; usually only one apical spot*tetrastigma* (Sepp)
5. Primaries below brown, with faint spot in space 8; secondaries below with pale bar at end of cell*eboneus* Δ Bell \square

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STUDIES ON THE NEARCTIC *EUCHLOE*

Part 3. COMPLETE SYNONYMICAL TREATMENT

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FULL SYNONYMIES ARE PRESENTED here for *Euchloe ausonides*, *Euchloe creusa*, *Euchloe hyantis*, and their named subspecific segregates. The author believed completeness to be essential so that future workers may refer to the material contained in past literature citations in light of the interpretations of these treatments.

Synonymical treatments for *Euchloe olympia* and *E. olympia rosa* are not presented at this time.

***Euchloe (Euchloe) ausonides* (Lucas)**

Anthocharis ausonides Lucas, 1852, Rev. Zool., 4(2nd ser.): 340; Boisduval, 1852, Ann. Soc. Ent. Fr., 2:X:286; Reakirt [*partim.*], 1866, Proc. Ent. Soc. Phil., 6:135; Herrich-Schaffer, 1867, Corr.-Blatt. Zool. Min. Ver. Regnsb., 21: 144; Boisduval, 1869, Ann. Soc. Ent. Belg., 12:40; Mead [*partim.*], 1875, in Wheeler, Rept. Geogr. Expl., 5:747; Moschler, 1878, Stett. Ent. Zeit., 39: 299, 309; Edwards, 1884, Trans. Amer. Ent. Soc., 9:261; Smith, 1891, List Lepid. Bor. Amer., p.13; Skinner [*partim.*] [erroneously includes the name *coloradensis* as a synonym], 1898, Syn. Cat. N. Amer. Rhop., p. 64; Grote, 1900, Proc. Am. Phil. Soc., 39:40; Skinner, 1903, in Smith, Chklst. Lepid. Bor. Amer., p. 9; Franck, 1905, Ent. News 16:28.

Anthocharis ausonides [*lapsus calami*]: Edwards [*partim.*], 1863, Proc. Ent. Soc. Phil., 2:81; Weidemeyer, 1863, Proc. Ent. Soc. Phil., 2:151; Edwards [*partim.*], 1897, Butt. N. Amer., 3:412.

Euchloe ausonides: Kirby, 1871, Syn. Cat. Di. Lepid., p. 340; Beutenmuller, 1898, Bull. Amer. Mus. Nat. Hist., 10:240-241, pl. 14, fig. 1; Holland [*partim.*], 1898, Butt. Book, p. 283, pl. 32, figs. 24, 25, pl. 34, fig. 3; Butler [*partim.*], 1899, Can. Ent., 31:19; Wright [*partim.*], 1906, Butt. West Coast, p. 104, figs. 56, 56b, 56c; Coolidge [*partim.*], [erroneously includes the name *coloradensis* as a synonym], 1908, Can. Ent., 40:298; Coolidge & Newcomes, 1908, Ent. News 19:204; Rober [*partim.*], 1909, in Seitz, Macrolepid., World 5:95, pl. 28, fig. a'; Barnes & McDunnough, 1916, Contr. Nat. Hist. Lepid. N. Amer., 3: 61-62; Barnes & McDunnough, 1917, Chklst. Lepid. Bor. Amer., p. 3; Barnes & Benjamin, 1926, Bull. So. Calif. Acad. Sci., 25:7; Comstock [*partim.*], 1927, Butt. Calif., p. 37, pl. 10, figs. 6, 9; Holland, 1931, Butt. Book, p. 284, pl. 32, figs. 24, 25, pl. 34, fig. 3; Martin & Ingham, 1931, Bull. So. Calif. Acad. Sci., 29: ; Davenport & Dethier, 1937, Ent. Amer. 17: 179; McDunnough [*partim.*], 1938, Mem. So.

- Calif. Acad. Sci., 1:7; Leighton [*partim.*], 1946, Univ. Wash. Pub. Biol., 9: ; Martin & Truxal, 1955, Los Angeles Co. Mus. Sci. Ser., 18 (Zool.), 8:5; Bird, 1956, Lepid. News 10:107; Ehrlich & Ehrlich [*partim.*], 1961, How to know Butt., p. 75, fig. ; Ehrlich & Ehrlich, 1962, Microent., 25(1):4.
- Anthocharis ausonia* var. *ausonoides* [*lapsus calami*]: Strecker, 1878, Syn. Cat. Macrolep., p. 77.
- Anthocrais ausonoides* [*lapsus calami*]: Hy. Edwards, 1880, Pacific Coast Lepid., 22; Hy Edwards, 1881, Papilio 1:51; von Osten-Sacken, 1882, Papilio 2: 29.
- Anthocaris ausonides*: Geddes, 1883, Can. Ent., 15:221.
- Euchloe* "variety from Vancouver", Butler [*partim.*], 1899, Can. Ent., 31:19.
- Synchloe ausonides*: Dyar, 1902, Bull. U.S. Nat. Mus., 52:7; Anderson, 1904, Cat. Brit. Col. Lepid., p. 6.
- Synchloe ausonoides* [*lapsus calami*]: Elrod & Maley [*partim.*], 1906, Bull. Univ. Montana 30 (Biol.): 32.
- Synchloe ausonides*: Elrod & Maley [*partim.*], 1906, Bull. Univ. Montana 30 (Biol.): 32.
- Euchloe creusa* (non Doubleday): Wright [*partim.*], 1906, Butt. West Coast, fig. 54b.
- Euchloe rosa* (non Edwards): Wright [*partim.*], 1906, Butt. West Coast, fig. 54c.
- Euchloe coloradensis* (non Hy. Edwards): Coolidge, 1908, Can. Ent., 40:299 (synonymy); Storer & Usinger, 1963, Sierra Nevada Nat. Hist., Univ. Calif. Press, p. 195.
- Euchloe belia* var. *creusa* (non Doubleday): Verity [*partim.*], 1908, Rhop. Pal., pl. 37, fig. 19.
- Euchloe belia* var. *creusa* gen. aest. *ausonides*: Verity [*partim.*], 1908, Rhop. Pal., pl. 37, fig. 20 [type], figs. 21, 22, 23, 24 .
- Euchloe ausonides* ♀ var. *flavidalis* Comstock [*partim.*], 1924, Bull. So. Calif. Acad. Sci., 23: 5; Comstock [*partim.*], 1927, Butt. Calif., p. 37, pl. 10, fig. 10 [TYPE].
- Euchloe ausonides* var. *semiflava* Comstock [*partim.*], 1924, Bull. So. Calif. p 37, pl. 10, fig. 11 [TYPE].
- Euchloe ausonides* ab. *semiflava*: Barnes & Benjamin [*partim.*], 1926, Bull. So. Calif. Acad. Sci., 25: 7; McDunnough [*partim.*], 1938, Mem. So. Calif. Acad. Sci., 1(1): 7; Leighton [*partim.*], 1946, Univ. Wash. Pub. Biol., 9: ; dos Passos [*partim.*], 1964, Lepid. Soc. Mem., 1:49.
- Euchloe ausonides* ab. *flavidalis*: Barnes & Benjamin [*partim.*], 1926, Bull. So. Calif. Acad. Sci., 25: 7; McDunnough [*partim.*], 1938, Mem. So. Calif. Acad. Sci., 1(1): 7.
- Euchloe ausonides coloradensis* (non Hy. Edwards): Comstock [*partim.*], 1927, Butt. Calif., p. 38; Brooks, 1942, Can. Ent., 74: 31; Martin & Truxal [*partim.*], 1955, Los Angeles Co. Mus. Sci. Ser., 18 (Zool.): 8:5; Garth & Tilden [*partim.*], 1963, J. Res. Lepid., 2:50.
- Euchloe ausonides* ab. *boharti* Doudoroff, 1930, Pan-Pac. Ent., 6: 143; McDunnough [*partim.*], 1938, Mem. So. Calif. Acad. Sci., 1(1): 7; dos Passos [*partim.*], 1964, Lepid. Soc. Mem., 1:49.
- Euchloe ausonides ausonides*: Talbot, 1932, Lepid. Catalogus 53:301; dos Passos [*partim.*], 1964, Lepid. Soc. Mem., 1:49.
- Euchloe ausonides* race *coloradensis* tr. f. [sic] *hemiflava* Field, 1936, J. Ent. & Zool., 28:19.
- Euchloe ausonides coloradensis* ab. *hemiflava*: McDunnough [*partim.*], 1938, Mem. So. Calif. Acad. Sci., 1(1): 7; Martin & Truxal [*partim.*], 1955, Los Angeles Co. Mus. Sci. Ser., 18 (Zool.), 8:5; dos Passos [*partim.*], 1964, Lepid. Soc. Mem., 1:49.
- Euchloe creusa orientalides* (non Verity): Martin & Truxal, 1955, Los Angeles Co. Mus. Sci. Ser., 18 (Zool.) 8:5.

Euchloe creusa lotta (non Beutenmuller): Garth & Tilden [*partim.*], 1963, J. Res. Lepid., pl. 58, fig. 1.

***Euchloe* (*Euchloe*) *ausonides coloradensis* (Hy. Edwards)**

Anthocharis ausonides [*lapsus calami*]: Edwards [*partim.*], 1863, Proc. Ent. Soc. Phil., 2:78; Edwards [*partim.*], 1897, Butt. N. Amer., 3:412.

Anthocharis ausonides: Reakirt [*partim.*], 1886, Proc. Ent. Soc. Phil., 6:135; Mead [*partim.*], 1875, in Wheeler, Rept. Geogr. Expl., 5:747; Mead, 1877, Psyche 2:182; Skinner, 1902, Trans. Amer. Ent. Soc., 29:37.

Anthocharis coloradensis Hy. Edwards 1881, Papilio 1:50.

Anthocharis ausonides coloradensis: Edwards, 1884, Trans. Amer. Ent. Soc., 9:261; Smith, 1891, List Lepid. Bor. Amer., p. 13; Skinner, 1903, Chklst. Lepid. Bor. Amer., p. 9.

Anthocharis ausonides var. *coloradensis*: Cockerell, 1899, Ent. Amer., 5:33.

Euchloe ausonides var. *coloradensis*: Beutenmuller [*partim.*], 1898, Bull. Amer. Mus. Nat. Hist., 10:241.

Euchloe coloradensis: Butler, 1899, Can. Ent., 31:19.

Synchlloe ausonides coloradensis: Dyar, 1902, Bull. U.S. Nat. Mus., 52:7.

Euchloe ausonides coloradensis: Wright, 1906, Butt. West Coast p. 104; Barnes & McDunnough, 1916, Contr. Nat. Hist. Lepid. N. Amer., 3:61; Barnes & McDunnough, 1917, Chklst. Lepid. Bor. Amer., p. 3; Barnes & Benjamin, 1926, Bull. So. Calif. Acad. Sci., 25:7; Comstock [*partim.*], 1927, Butt. Calif., pl. 10, figs. 13, 14; Klots, 1930, Bull. Brook. Ent. Soc., 25:154; Holland, 1931, Butt. Book p. 284; Talbot, 1932, Lepid. Catalogus 53:302; Cross, 1937, Proc. Colo. Mus. Nat. Hist., 16:7; McDunnough [*partim.*], 1938, Mem. So. Calif. Acad. Sci., 1(1):7; Brown, 1955, Proc. Denver Mus. Nat. Hist., 6:181; Martin & Truxal [*partim.*], Los Angeles Co. Mus. Sci. Ser., 18(Zool.), 8:5; Defoliart, 1956, Lepid. News 10:99; dos Passos [*partim.*] [erroneously includes the name *hemiflava* as a synonym], 1964, Lepid. Soc. Mem., 1:49.

Euchloe belia var. *belioides* race *montana* Verity, 1908, Rhop. Pal., pl. 68, figs. 13, 14, 15.

Euchloe ausonides montana: Barnes & McDunnough, 1917, Chklst. Lepid. Bor. Amer., p. 3 [synonymy]; Barnes & Benjamin, 1926, Bull. So. Calif. Acad. Sci., 25:7 [synonymy]; Holland, 1931, Butt. Book p. 284 [synonymy]; McDunnough, 1938, Mem. So. Calif. Acad. Sci., 1(1):7 [synonymy]; dos Passos, 1964, Lepid. Soc. Mem., 1:49 [synonymy].

Euchloe ausonides coloradensis ab. *hemiflava* (non Field): Martin & Truxal [*partim.*], 1955, Los Angeles Co. Mus. Sci. Ser., 18(Zool.), 8:5.

Euchloe ausonides (non Lucas): Maeki & Remington, 1960, J. Lepid. Soc., 14: 42, 52; Ehrlich & Ehrlich [*partim.*], 1961, How to Know Butt., p. 75; Ehrlich, 1961 Microent., 24(4):138.

Euchloe ausonides race *mayi* Chermock & Chermock, 1940, Can. Ent., 72:82.

***Euchloe* (*Euchloe*) *ausonides mayi* Chermock & Chermock**

Euchloe ausonides mayi: Brooks, 1942, Can. Ent., 74:32; dos Passos, 1964, Lepid. Soc. Mem., 1:49.

Anthocharis creusa Doubleday, 1847, Gen. Di. Lepid., 1:56, pl. 7, fig. 1; Weidemeyer, 1863, Proc. Ent. Soc., Phil., 2:151; Herrich-Schaffer, 1867, Corr.-Blatt. Zool. Min. Ver. Regnsb., 21:144; Smith, 1891, List Lepid. Bor. Amer., p. 13; Skinner, 1898, Syn. Cat. N. Amer. Rhop., p. 64; Skinner, 1903, in Smith, Chk. Lst. Lepid. Bor. Amer., p. 9.

Euchloe creusa: Kirby, 1871, Syn. Cat. Di. Lepid., p. 340; Beutenmuller, 1897, J. N.Y. Ent. Soc., 5:208; Beutenmuller [*partim.*], 1898, Bull. Amer. Mus. Nat. Hist., 10:16; Butler, 1899, Can. Ent., 31:56; Coolidge, 1908, Can. Ent., 40:299; [?] Rober, 1909, in Seitz, Macrolepid. World 5:95, pl. 28, fig. a"; Barnes & McDunnough, 1916, Contr. Nat. Hist. Lepid. N. Amer., 3:59; Barnes & McDunnough, 1917, Chklst. Lepid. Bor. Amer., p. 3; Barnes & Benjamin [*partim.*] [authors erroneously

include the name *pumilio* as a synonym], 1926, Bull. So. Calif. Acad. Sci., 25:7; McDunnough [*partim.*] [erroneously includes the name *pumilio* as a synonym], 1938, Mem. So. Calif. Acad. Sci., 1:17; Martin & Truxal, 1955, Los Angeles Co. Mus. Sci. Ser., 18(Zool.), 8:5; Ehrlich & Ehrlich [*partim.*] [authors erroneously include Alberta in statement of distribution], 1961, How to Know Butt., p. 75; dos Passos [*partim.*] [incorrectly includes the name *pumilio* as a synonym], 1964, Lepid. Soc. Mem., 1:49.

Anthocaris crensa [*lapsus calami*]: Edwards, 1881, Papilio 1:51.

Euchloe creusa var. *elsa* Beutenmuller [*partim.*], 1898, Bull. Amer. Mus. Nat. Hist., 10:342, pl. 14, fig. 3; Beutenmuller [*partim.*], 1899, Can. Ent., 31:56.

Euchloe elsa: Butler, 1899, Can. Ent., 31:19 [synonymy]; Coolidge, 1898, Can. Ent., 40:299 [synonymy]; Barnes & McDunnough, 1916, Contr. Nat. Hist. Lepid. N. Amer., 3:59 [synonymy]; Barnes & McDunnough, 1917, Chklst. Lepid. Bor. Amer., p. 3 [synonymy]; Barnes & Benjamin, 1926, Bull. So. Calif. Acad. Sci., 25:7 [synonymy]; Holland [*partim.*], 1931, Butt. Book p. 285 [synonymy]; McDunnough [*partim.*], 1938, Mem. So. Calif. Acad. Sci., 1:7 [synonymy]; dos Passos [*partim.*], 1964, Lepid. Soc. Mem., 1:49 [synonymy].

Synchlœ creusa: 1904, Anderson, Cat. Brit. Col. Lepid., p. 6.

Euchloe belia var. *orientalides* Verity [*partim.*], 1908, Rhop. Pal., pl. 36, fig. 58.

Euchloe belia var. *creusa* Verity [*partim.*], 1908, Rhop. Pal., pl. 68, figs. 11, 13 ("COTYPES") [As mentioned in Barnes & McDunnough, 1916, verified through correspondence with Dr. N. D. Riley of the British Museum, 1964, these two figures represent the dorsal and ventral surfaces of the single type specimen].

Euchloe creusa orientalides: Barnes & McDunnough [*partim.*], 1917, Chklst. Lepid. Bor. Amer., p. 3; Barnes & Benjamin [*partim.*], 1926, Bull. So. Calif. Acad. Sci., 25:7; McDunnough [*partim.*], 1938, Mem. So. Calif. Acad. Sci., 1:7; dos Passos [*partim.*], 1964, Lepid. Soc. Mem., 1:49.

Euchloe (Euchloe) creusa: Klots, 1930, Bull. Brook. Ent. Soc., 25:87.

Euchloe creusa creusa: Talbot [*partim.*], 1932, Lepid. Catalogus 53:302.

Euchloe creusa creusa ab. *elsa*: Talbot [*partim.*], 1932, Lepid. Catalogus 53:302.

***Euchloe (Euchloe) hyantis hyantis* (Edwards)**

Anthocharis hyantis Edwards, 1871, Trans. Amer. Ent. Soc., 3:205; Mead, 1877, Psyche, 2:182; Butler [*partim.*], 1882, J. Linn. Soc., 16:471; Edwards [*partim.*], 1884, Trans. Amer. Ent. Soc., 9:260; Smith, 1891, List Lepid. Bor. Amer., p. 13; Edwards, 1892, Can. Ent., 24:109; Skinner, 1903, in Smith, Chklst. Lepid. Bor. Amer., p. 9.

Anthocaris hyantis: Hy. Edwards [*partim.*] [erroneously treats the name *creusa* as a synonym], 1880, Pac. Coast Lepid., 22; Hy. Edwards, 1880, Pac. Coast Lepid., 28; Edwards, 1881, Papilio 1:51; von Osten Sacken, 1882, Papilio, 2:29.

Anthocaris creusa: Hy. Edwards, 1880, Pac. Coast Lepid., no. 22 [synonymy].

Euchloe hyantis: Butler [*partim.*], 1882, J. Linn. Soc., 16:471; Beutenmuller, 1897, J. N.Y. Ent. Soc., 5:208; Butler, 1899, Can. Ent., 31:19; Beutenmuller, 1899, Can. Ent., 31:56; Coolidge [*partim.*], 1908, Can. Ent., 40:298; [?] Rober, 1909, in Seitz, Macrolepid. World pl. 28, fig. a"; Holland [*partim.*], 1931, Butt. Book, rev. ed., pl. 67, fig. 27 ["TYPE"]; Storer & Usinger, 1963, Sierra Nevada Nat. Hist., pl. 67, fig. 72.

Euchloe creusa: Beutenmuller [*partim.*], 1898, Bull. Amer. Mus. Nat. Hist., 10:241, pl. 14, fig. 2.

Anthocharis ausonides var. *hyantis*: Skinner, 1898, Syn. Cat. N. Amer. Rhop., p. 64.

Anthocharis ausonides hyantis: Franck, 1905, Ent. News, 16:28 [synonymy].

Anthocharis ausonides coloradensis: Franck, 1905, Ent. News, 16:29 [synonymy].

Euchloe creusa var. *hyantis*: Coolidge [*partim.*], 1908, Can. Ent., 40:298.

Euchloe belia var. *creusa* (non Doubleday): Verity, 1908, Rhop. Pal., pl. 37, fig. 16.

Euchloe creusa cum. ab. [*sic!*] *pumilio* Strand [*partim.*], 1914, Archiv. f. Naturgesch., 80(A 11):153.

Euchloe creusa hyantis: Barnes & McDunnough, 1916, Contr. Nat. Hist. Lepid. N. Amer., 3:60; Barnes & McDunnough [*partim.*], 1917, Chklst. Lepid. Bor. Amer., p. 3; Barnes & Benjamin [*partim.*], 1926, Bull. So. Calif. Acad. Sci., 25:7; Comstock [*partim.*], 1927, Butt. Calif., p. 38; Talbot, 1932, Lepid. Catalogus 53:302; McDunnough [*partim.*], 1938, Mem. So. Calif. Acad. Sci., 1:7; Martin & Truxal [*partim.*], 1955, Los Angeles Co. Mus. Sci. Ser., 18(Zool.), 8:5; Garth & Tilden, 1963, J. Res. Lepid., 2:50, 87; dos Passos [*partim.*], 1964, Lepid. Soc. Mem., 1:49.

Euchloe creusa pseudoausonides: Barnes & McDunnough, 1916, Contr. Nat. Hist. Lepid. N. Amer., 3:61 [synonymy]; Barnes & McDunnough, 1917, Chklst. Lepid. Bor. Amer., p. 3 [synonymy]; Barnes & Benjamin, 1926, Bull. So. Calif. Acad. Sci., 25: [synonymy]; McDunnough, 1938, Mem. So. Calif. Acad. Sci., 1:7 [synonymy]; dos Passos, 1964, Lepid. Soc. Mem., 1:49 [synonymy].

Euchloe creusa orientales: Barnes & McDunnough, 1916, Contr. Nat. Hist. Lepid. N. Amer., 3:61 [synonymy]; Barnes & McDunnough [*partim.*], 1917, Chklst. Lepid. Bor. Amer., p. 3; Barnes & Benjamin [*partim.*], 1926, Bull. So. Calif. Acad. Sci., 25:7; McDunnough [*partim.*] 1938, Mem. So. Calif. Acad. Sci., 1:7; dos Passos [*partim.*], 1964, Lepid. Soc. Mem., 1:49.

Euchloe ausonides andrewsi (non Martin): Powell, 1958, Lepid. News, 12:28.

***Euchloe* (*Euchloe*) *hyantis andrewsi* (Martin) NEW COMBINATION**

Euchloe ausonides race *andrewsi* Martin, 1936, Bull. So. Calif. Acad. Sci., 35:94.

Euchloe ausonides andrewsi: Martin & Truxal, 1955, Los Angeles Co. Mus. Sci. Ser., 18(Zool.), 8:5; dos Passos, 1964, Lepid. Soc. Mem., 1:49.

***Euchloe* (*Euchloe*) *hyantis lotta* (Beutenmuller), NEW COMBINATION**

Anthocharis creusa (non Doubleday): Strecker, 1878, Syn. Cat. Macrolepid., p. 77.

Anthocharis hyantis (non Edwards): Morrison, 1883, Papilio 3:9; Edwards [*partim.*], 1884, Trans. Amer. Ent. Soc., 9:260.

Euchloe lotta Beutenmuller, 1898, Bull. Amer. Mus. Nat. Hist., 10:24, pl. 14, fig. 4; Butler, 1899, Can. Ent., 31:56; Wright [*partim.*], 1906, Butt. West Coast, p. 104; Holland [*partim.*], 1931, Butt. Book, rev. ed., p. 285, pl. 73, fig. 5 ["TYPICAL", text], ["PARATYPE", plate legend].

Euchloe creusa (non Doubleday): Holland [*partim.*], 1898, Butt. Book, p. 283, pl. 32, fig. 23, pl. 34, fig. 2; Wright [*partim.*], 1906, Butt. West Coast, p. 194, figs. 54, 54a; Klots, 1930, Bull. Brook. Ent. Soc., 25: 153; Holland [*partim.*], 1931, Butt. Book, rev. ed., pl. 32, fig. 23, pl. 34, fig. 2; Leighton [*partim.*], 1946, Univ. Wash. Pub. Biol., 9: ; Bauer, 1953, Lepid. News 7:146; Brown, 1955, Proc. Denver Mus. Nat. Hist., 6:182; Ehrlich & Ehrlich [*partim.*], 1961, How to Know Butt., p. 75, fig.

Euchloe ausonides var. *lotta*: Browning, 1901, Ent. News, 12(10):301, fig. 5.

- Synchloe creusa* (non Doubleday): Dyar [partim.], 1902, Bull. U.S. Nat. Mus., 52:7.
- Synchloe lotta*: Dyar [partim.], 1902, Bull. U.S. Nat. Mus. 52:7.
- Anthocharis lotta*: Skinner, 1903, in Smith, Chklst. Lepid. Bor. Amer., p. 9.
- Euchloe hyantis* (non Edwards): Wright [partim.], 1906, Butt. West Coast, p. 104; Strand [partim.], 1914, Archiv. f. Naturgesch., 80(A 11):153; Holland [partim.], 1931, Butt. Book, rev. ed., p. 285.
- Euchloe rosa* (non Edwards): Wright [partim.], 1906, Butt. West Coast, p. 104, figs. 56, 56b.
- Euchloe belia* var. *orientalides* Verity [partim.], 1908, Rhop. Pal., pl. 36, fig. 58.
- Euchloe creusa* var. *lotta*: Coolidge, 1908, Can. Ent., 40:299.
- Euchloe belia* var. *creusa* (non Doubleday): Verity [partim.], 1908, Rhop. Pal., pl. 37, figs. 17, 18.
- Euchloe creusa* cum. ab. [sic!] *pumilio* Strand [partim.], 1914, Archiv. f. Naturgesch., 80(A 11):153.
- Euchloe creusa lotta*: Barnes & McDunnough, 1916, Contr. Nat. Hist. Lepid. N. Amer., 3:61; Barnes & McDunnough, 1917, Chklst. Lepid. Bor. Amer., p. 3; Barnes & Benjamin, 1926, Bull. So. Calif. Acad. Sci., 25:7; Comstock [partim.], 1927, Butt. Calif., p. 38, pl. 10, figs. 7, 8; Gunder, 1930, Bull. So. Calif. Acad. Sci., 29:9; Comstock & Dammers, 1932, Bull. So. Calif. Acad. Sci., 31:35; Talbot, 1932, Lepid. Catalogus 53:302; Davenport & Dethier [partim.], 1937, Ent. Americana 17:179; McDunnough, 1938, Mem. So. Calif. Acad. Sci., 1(1):7; Martin & Truxal [partim.], 1955, Los Angeles Co. Mus. Sci. Ser., 18(Zool.), 8:5; Garth & Tilden [partim.], 1963, J. Res. Lepid., pl. 5, fig. N; dos Passos, 1964, Lepid. Soc. em., 1:49.
- Euchloe belioides*: Barnes & McDunnough, 1916, Contr. Nat. Hist. Lepid. N. Amer., 3:61 [synonymy]; Barnes & McDunnough, 1917, Chklst. Lepid. Bor. Amer., p. 3 [synonymy]; Barnes & Benjamin, 1926, Bull. So. Calif. Acad. Sci., 25:7 [synonymy]; Holland, 1931, Butt. Book, rev. ed., p. 285 [synonymy]; McDunnough, 1938, Mem. So. Calif. Acad. Sci., 1(1):7 [synonymy]; dos Passos, 1964, Lepid. Soc. Mem., 1:49 [synonymy].
- Euchloe creusa hyantis* (non Edwards): Coolidge, 1925, Ent. News, 36:65; Comstock [partim.], 1927, Butt. Calif., p. 38, pl. 10, figs. 4, 5; Davenport & Dethier [partim.], 1937, Ent. Americana 17:179; Leighton [partim.], 1946, Univ. Wash. Pub. Biol., 9: ; Martin & Truxal [partim.], 1955, Los Angeles Co. Mus. Sci. Ser., 18(Zool.), 8:5.
- Euchloe creusa* ab. *pumilio*: Strand, 1927, Bull. Soc. Zool. France 51:412.

STUDIES ON THE NEARCTIC *EUCHLOE*

Part 4. TYPE DATA AND TYPE LOCALITY RESTRICTIONS¹

IN ANY TAXONOMIC REVISION, it is important for the revisor to know the biological identity and the type locality of the insect with which he is dealing. As a direct result of this precept, the information concerning the types of the named entities of Nearctic *Euchloe*, which are considered to be biologically applicable by this author, is presented in this paper. Also, the type localities

¹ F. M. Brown, Colorado Springs, Colorado and J. A. Powell, University of California, Berkeley, California kindly read the manuscript of this paper and offered several helpful suggestions.

of three named taxa are restricted so as to provide a base for logical discussion of the distributional limits and the geographic variability of these units and their associated populations.

For each name, the citation of the original description, a compendium of the available information concerning the type, and an interpretation of the type information are presented.

Euchloe (Euchloe) ausonides (Lucas)

CITATION OF ORIGINAL DESCRIPTIONS Lucas, 1852. *Rev. Mag. Zool.* 4(2nd series):324-345.

TYPE DATA: The holotype is in the collection of the United States National Museum, Washington, D.C. The specimen is *ex* collection Barnes, *ex* collection Oberthur, and *ex* collection Boisduval. Dr. Jerry A. Powell of the University of California at Berkeley examined the type specimen and obtained the data which are presented below.

The specimen, which lacks the right forewing and both antennae, has a forewing costal measurement [base to apex] of 24.3 millimeters. The forewing discal spot is 1.2 millimeters in width at the middle and has fairly heavy whitish overscaling along the vein at the upper edge of the cell.

The specimen bears five labels as follows: 1./"Ex Musaeo Dris Boisduval" machine printed label with black border, 2./"Oberthur Collection" machine printed label with red border, 3./"Figure par R. Verity/Rhopal. Palaearctica P1 XXXVII, fig. 20", 4./"Anthocharis Ausonides, Boisd., Lepid. Californie, II Partie, St. Entom. Belgiq. 1869 p. 40" handwritten label, 5./"Type *ausonides* Bdv. a/c Hofer 1925FHB" handwritten label with red border, different hand than 4.

INTERPRETATION OF TYPE DATA: That this is the type specimen described by Lucas is substantiated by the fact that the costal measurement of this unusually large male specimen is in close agreement with the measurement given by Lucas (1852).

The specimen was part of the first lot of material sent to Boisduval by P. J. M. Lorquin who collected the material for that shipment in central California. Since Lucas, as well as Boisduval, stated nothing further than "California" as the type locality, since there are populations of this species occurring in California with significantly varying phenotypic expression, and since Lorquin could well have collected the specimen in the San Francisco Bay area, the type locality is hereby restricted to San Francisco, San Francisco County, California.

Euchloe (Euchloe) ausonides coloradensis (Hy. Edwards)

CITATION OF ORIGINAL DESCRIPTION: Hy. Edwards, 1881. *Papilio* 1(4):50-55.

TYPE DATA: The holotype is in the American Museum of Natural History, New York. The specimen bears the following labels: 1./AMNH catalogue number "3577" on which the word "Colorado" is appended, 2./The original Henry Edwards label bears the catalogue number "14".

INTERPRETATION OF TYPE DATA: The following information was supplied by F. M. Brown (personal communication). In his catalogue under entry "14", Henry Edwards noted, "*ausonides* Bdv. pastures Alameda Co. Calif. etc. HE 3-5, settles on flowers of *Sinapis* [= *Brassica*]." Brown states that the "14" on the type specimen means that Henry Edwards at first considered the specimen to be the same as the material he collected in California from March through May. Brown, who examined the type specimen at the request of the author, sent the accompanying analysis which is quoted in part below.

The specimen is without doubt one sent to Henry Edwards by W. H. Edwards from the material collected by T. L. Mead in 1871. In a letter from W.H.E. to Hy. E. dated July 8, 1871 about Mead specimens being sent to Hy. Edw., Edwards states 'And *Anthocaris* 1 is *Ausonides*. The *Anthocaris* 2 is new if it is not *Reakirtii*.' The date of the letter places the capture in June. Mead (1875: 747-748) confirms this.

From the itinerary of Mead pieced together by Brown (1955), it is seen that in June, 1871, Mead traveled from Denver to Fairplay via Morrison, Turkey Creek Junction, Bailey, and Kenosha House, whereupon he returned to Turkey Creek Junction by the same route. He then remained at Turkey Creek for a week (June 20-27, 1871) before moving elsewhere. Coolidge and Newcomer (1908) quote from a letter written by Mead to W. H. Edwards in which Mead told about finding the eggs and larvae of *Euchloe ausonides coloradensis* at Turkey Creek Junction. From the information supplied by Brown, including a suggestion that Turkey Creek Junction would be a good type locality, and the fact that it is known that Mead found eggs and larvae of *Euchloe ausonides coloradensis* at Turkey Creek Junction, the type locality of *Euchloe ausonides coloradensis* is hereby restricted to Turkey Creek Junction, Jefferson County, Colorado.

***Euchloe (Euchloe) creusa creusa* (Doubleday)**

CITATION OF ORIGINAL DESCRIPTIONS Doubleday, 1847. *Gen. Di. Lepid.* 1:56, pl. 7, fig. 1.

TYPE DATA: The original citation stated only that the type was collected in the Rocky Mountains of North America, there was no description, and the plate figure is a barely recognizable draw-

ing. N. D. Riley of the British Museum of Natural History, in whose institution the holotype specimen is located, supplied the author with the necessary information concerning the type. The specimen bears two labels: 1./"Rocky Mountains 45-135", 2./"Rhopalocera Palaearctica".

INTERPRETATION OF TYPE DATA: Riley (personal communication) states that the first label which was mentioned above indicates that the specimen was presented in 1845 by the then Earl of Derby. F. M. Brown (personal communication) states that "the great majority of North American specimens collected by Lord Derby came from the vicinity of Banff, Alberta. I doubt that he got over to the B.C. side of the range and it is questionable that he got as far north as Kicking Horse Pass." The second label shows that the specimen was figured by Verity (1908); the dorsal and the ventral surfaces of the type specimen are shown as figures 11 and 12 on plate 68. Taking into consideration the previously stated judgements of Brown, as well as those of Barnes and McDunnough (1916) and McHenry (personal communication), and the fact that specimens readily assignable to the holotype have been collected near Banff, the type locality of *Euchloe creusa* Doubleday is hereby restricted to the vicinity of Banff, near 7,000' elevation, Alberta, Canada.

***Euchloe (Euchloe) hyantis hyantis* (Edwards)**

CITATION OF ORIGINAL DESCRIPTION: Edwards, 1871 *Trans. Amer. Ent. Soc.* 3:205-216.

TYPE DATA: In the original citation it was stated that the type material was collected at Mendocino, California by R. H. Stretch. Specimens designated as types are located in the collection of the Carnegie Museum, Pittsburgh, Pennsylvania. H. K. Clench (personal communication) states that there is a specimen labeled as follows: "*Hyantis* ♀ / type Cala" written in the hand of W. H. Edwards, the word "type" in red, the rest in black. A pin with an identical label except ♂ with a fragment of thorax on it is next to the supposed allotype.

INTERPRETATION OF TYPE DATA: "Mendocino, California" is now known as Mendocino City, Mendocino County, California. The significance of the red and the black ink on the type labels pertains to the context of the time when they were written. According to F. M. Brown the notations in black were probably written in 1889 or sometime later when Edwards shipped the specimens to Holland. The story of the word "type" written in red ink, according to Clench (personal communication), is that after Holland had purchased Edwards' collection he removed the labels from the specimens that he considered to be types and

returned them to Edwards, who wrote the word "type" on them in red ink. He subsequently returned them to Holland who replaced the labels on the appropriate specimens. It should also be noted that the original description stated "In the collection of Hy. Edwards". Although this collection is under the care of the American Museum of Natural History, specimens designated as types of *hyantis* are not to be found in that institution. The above situation cannot be resolved at this time and a final decision of the proper types of *hyantis* must be held in abeyance.

***Euchloe (Euchloe) hyantis lotta* Beutenmuller**

CITATION OF ORIGINAL DESCRIPTION: Beutenmüller, 1898. *Bull. Amer. Mus. Nat. Hist.* 10(13):243, pl. 14, fig. 4.

TYPE DATA: Neither a type specimen nor a type locality was designated in the original paper. The distribution which was given as "Colorado, Arizona, Utah, Southern California", and a drawing are sufficient to delineate, in the gross sense, the entity to which this name should apply. There is a specimen figured by Holland (1931) as figure 5 on plate 73 which is referred to by him in the text as "paratype" and on the plate legend as "typical". The specimen is in the Carnegie Museum and bears the following labels: 1./"P.----- ♂, Arizona" (in pen, possibly in the hand of W. H. Edwards), 2./"lotta" (typewritten), 3./"Butterfly Book, Plate 73 Fig. 5" (the underlined numerals written in pen) (Clench, personal communication).

INTERPRETATION OF TYPE DATA: The problem now arises whether the above specimen is a syntype loaned by Beutenmüller to Holland for illustration in his book as was done with "*Thecla ilavia*" Beutenmüller (P. McHenry, personal communication), or if the specimen was selected by Holland from the W. H. Edwards material and was never seen by Beutenmüller. If the latter case were true the specimen is NOT an eligible candidate for a lectotype. Thus, the situation of the absence of a suitable lectotype prevents one from restricting the type locality with any exactness.

***Euchloe (Euchloe) hyantis andrewsi* Martin**

CITATION OF ORIGINAL DESCRIPTION: Martin, 1936. *Bull. So. Calif. Acad. Sci.* 35(2):94-95.

TYPE DATA: All of the type material was collected along the Crestline Highway, near Lake Arrowhead, San Bernardino Mountains, San Bernardino County, California between the elevations of 5000' and 6000' by R. H. Andrews on the dates June 14-19, 1935 and June 8-18, 1936. The holotype, allotype, and 37 paratypes are located in the Los Angeles County Museum, Los Angeles, California.

Euchloe (Euchloe) ausonides mayi Chermock & Chermock

CITATION OF ORIGINAL DESCRIPTION: Chermock & Chermock, 1940. *Can. Ent.* 72(4):81-83.

TYPE DATA: Holotype male, Riding Mountains, Manitoba, Canada, June 12, 1933, collected by Jack F. May. The specimen is in the collection of F.H. Chermock. The allotype female is located in the collection of the Carnegie Museum, Pittsburgh, Pennsylvania. The information of the accompanying labels of the allotype was noted for the author by H. K. Clench of the above institution: 1./"Riding Mountains/Manitoba VII-31-33" locality in letterpress, date handwritten, 2./"*Euchloe ausonides*/ var. *mayi*/ allotype / F. H. Chermock/ R. L. Chermock" the two authors names in script, the rest hand-lettered, all in black ink on a hand bordered pink card.

In the paper which included the original description the authors stated that 100 paratypes, all from the same locality but with various dates, were designated. Three paratypes are known to be located in the American Museum of Natural History, and one paratype is in the Carnegie Museum.

Euchloe (Euchloe) olympia (Edwards)

CITATION OF ORIGINAL DESCRIPTION: Edwards, 1871. *Trans. Ameri. Ent. Soc.* 3:266-277.

TYPE DATA: The holotype and allotype are located in the Carnegie Museum, Pittsburgh, Pennsylvania. The following information was provided through the courtesy of H.K. Clench of the Carnegie Museum. Each specimen bears the label: "Olympia ♂ [or ♀] / type Kan ". The word "type" is NOT in red ink.

INTERPRETATION OF TYPE DATA: The fact that the word "type" is not in red ink probably signifies that the word was placed on the labels at the time of the original description, and that these labels were NOT sent to Edwards by Holland at a much later date to have the word "type" appended in red ink (*fide* Clench, personal communication). The cryptic Kana refers to Kanawha according to Clench (personal communication), who states that "the name is born by a country, a river, and at least three communities or post offices have it as part of their name." Klots (1951) cites the type locality as Coalburgh, West Virginia. F. M. Brown (personal communication) states that Edwards lived in Coalburgh on the Kanawha River and often collected there. Hence, to be precise and in agreement with the data on the type label, the type locality should be stated as "banks of the Kanawha River, near Coalburgh, West Virginia."

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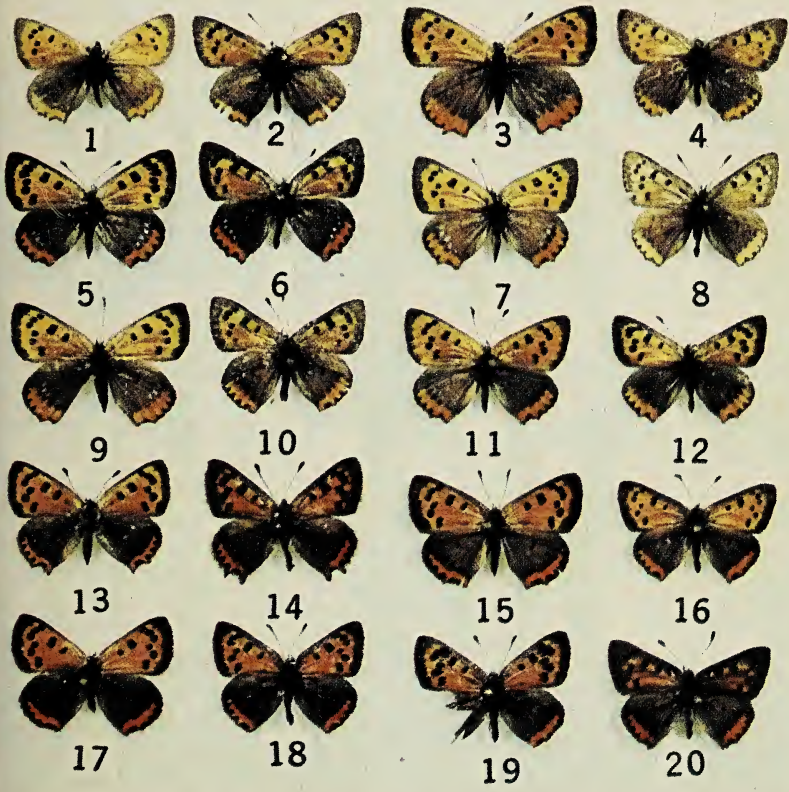
IN THIS ISSUE

Laboratory Techniques for Maintaining Cultures of the Monarch Butterfly	F. A. Urquhart and R. W. Stegner	129
Vital Staining of <i>Colias philodice</i> and <i>C. eurytheme</i>	John M. Kolyer	137
The North American Species of the Genus <i>Zeiraphera</i>	A. Mutuura and T. N. Freeman	153
Notes on <i>Eacles penelope</i> (Saturniidae)	Brian O. C. Gardiner	177
Remarks on The Genus <i>Zera</i> Evans in Mexico with a New Record	H. A. Freeman	181
Studies on the Nearctic <i>Euchloe</i>		
Part 3. Complete Synonymical Treatment		185
Part 4. Type Data and Type Locality Restrictions	Paul A. Opler	190



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THE PURPOSE OF THE JOURNAL is to combine in one source the work in this field for the aid of students of this group of insects in a way not at present available. THE JOURNAL will attempt to publish primarily only critical and complete papers of an analytical nature, though there will be a limited section devoted to shorter papers and notes. QUALITY WORK on any aspects of research on the Lepidoptera is invited. Analytical and well illustrated works are preferred, with a minimum of long description.

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A NEW SPECIES OF *ONCOCNEMIS*
FROM THE WESTERN UNITED STATES
(NOCTUIDAE:CUCULLIINAE)

JOHN S. BUCKETT AND WILLIAM R. BAUER

University of California, Davis, and
State Department of Agriculture, Sacramento

FOR MANY YEARS THE AUTHORS have possessed a series of an *Oncocnemis* species that was believed to be new. Until recently, we were under the opinion that this new species was probably most closely related to *O. hayesi* Grote, as it superficially resembled that species more than it did any other species within the genus. Much to our surprise, when genitalic mounts of both sexes had been prepared and critically examined, it became apparent that the superficial resemblance to *hayesi* had been misleading. With further examination of other species in this section of the genus, it was found that *O. melantho* Smith, described from specimens collected in the Yosemite Valley, California, was extremely closely related to *O. sandaraca* Buckett and Bauer, herein described as new.

Both *O. melantho* and *O. sandaraca* occur sympatrically at various localities in the central Sierra Nevada, and the adults rely, in part at least, on the same species of Rabbit brush (*Chrysothamnus* spp.) as a food source. Both species occur where there is floral influence of the Great Basin type. It is also interesting to note that while both species occur diurnally on flowers, only *sandaraca* has been taken nocturnally. The frequency of *sandaraca* occurring during diurnal hours is much less than that for *melantho*.

***Oncocnemis sandaraca* Buckett and Bauer, new species**

Male: Ground color of primaries dorsally yellowish-red (thus the name *sandaraca*, from Latin), transverse lines and marks conspicuous; secondaries dorsally a pale yellow with black exterior band. Head with vertex clothed in bicolorous elongate flattened dentate hairs, basally tan, apically brown; between vertex and frons a dark brown transverse band is evident; frons clothed in tan simple hairs; palpi exterolaterally clothed pre-



Fig. 1. Distribution map of *Oncocnemis sandaraca* Buckett and Bauer showing known distribution.



2



3

Fig. 2. Holotype male, *O. sandaraca*, dorsal view. Johnsville, Plumas County, California, 6 September 1959, ex. fluorescent black light (W. R. Bauer & J. S. Buckett).

Fig. 3. Allotype female, *O. sandaraca*, dorsal view. Same locality and collectors as in fig. 2, 8 September 1960.



4



5

Fig. 4. Male, *O. melantho* Smith, dorsal view. Road to Spencer Lakes, 8 miles southwest of Johnsville, Plumas County, California, 10 September 1961 (W. R. Bauer & J. S. Buckett).

Fig. 5. Female, *O. melantho*, dorsal view. 13 miles northeast of Garden Valley, Boise County, Idaho, 27 August 1965 (W. R. Bauer, J. S. Buckett & M. R. Gardner).

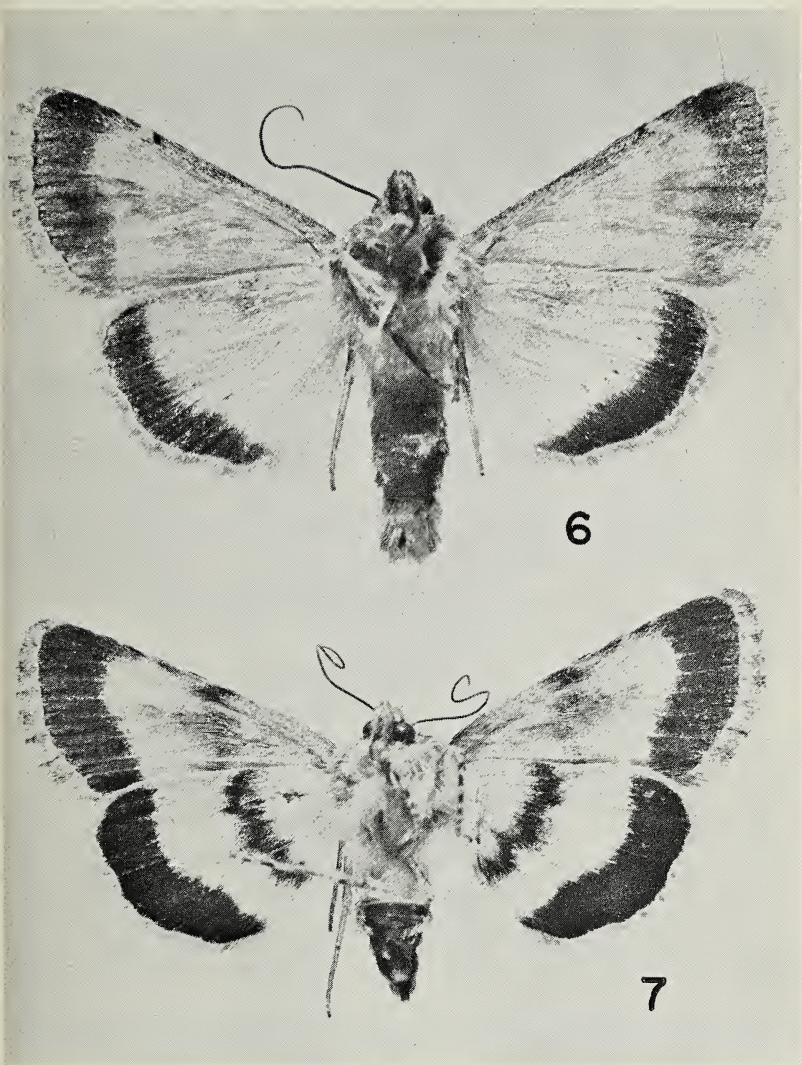


Fig. 6. Holotype male, *O. sandaraca*, ventral view. Data same as for fig. 2.

Fig. 7. Female, *O. melantho*, ventral view. Data same as for fig. 5.

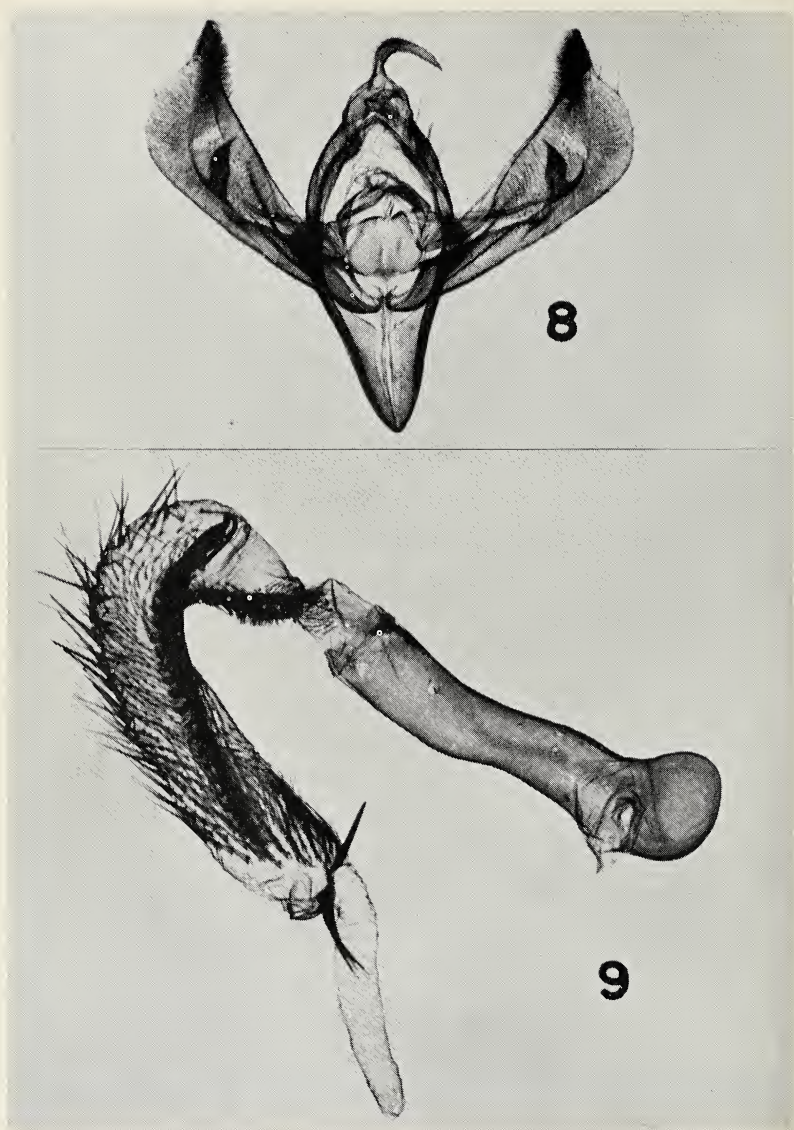


Fig. 8. Paratype male, *O. sandaraca*, genitalia minus aedeagus. Johnsville, Plumas County, California, 10 October 1966 (H. J. Pini), Bauer-Buckett Slide No. 66L19-3.

Fig. 9. Paratype male, *O. sandaraca*, aedeagus. Data same as for fig. 8.

dominantly in tan simple scales, but a few brown scales present also, ventrally clothed in elongate tan and brown simple hairs; terminal segment of palpi short, clothed in brown scales; compound eyes weakly fringed dorsally and posteriorly with tan tipped brown simple hairs or "lashes"; antennae with scape and pedicel clothed in tan scales; flagellomeres brown, dorsally clothed weakly in tan-brown scales, ventrally weakly ciliate, ciliations becoming more pronounced apically. Thorax with collar tricolor, composed of elongate scales, basally and apically yellowish-red, medially brown so as to form a transverse band; tegulae clothed in white, tan, brown, and dark brown simple hairs and elongate scales, appearing most lightly colored inwardly (border near disc); as in tegulae except possessing a greater percentage of simple hairs vs. elongate scales; posterior tuft composed of tan colored elongate scales; ventrally clothed in light tan simple, elongate hairs; legs with femora dorsally clothed in tan and brown scales and hairs, ventrally clothed in elongate ochreous and tan simple hairs; tibiae with tibial claw pronounced; meso and meta tibiae dorso-basally clothed with a bunch of elongate tan simple hairs, dorso-apically clothed in mixture of tan and dark brown scales; tarsi predominantly clothed in black scales, but each segment possessing an apical annulus of tan scales; primaries dorsally of ground color; costal subcostal and radial veins clothed in ochreous except where transverse lines intersect costa; basal one-half line geminate on costa, basally brown, apically ochreous; basal and transverse anterior areas contiguous, clothed in reddish-yellow scales; transverse anterior line geminate, basally ochreous, apically brown, strongly marked costally, thence undulating to inner margin; median area with conspicuous brown transverse shade, strongly marked costally, also dark brown scaling present on Cu_1 and $2dA$ veins; orbicular round, outlined in dark brown, thence ochreous, centrally overlain with brownish scales; reniform trapazoidal, broadest apically, narrowest basally; transverse posterior line geminate on costa, dark brown, centrally filled with ochreous, thence a single brown undulating line separating dark median area from yellowish-red portion of subterminal area; subterminal area basally more ochreous in area of radial and medial veins and more yellowish-red in area of cubital veins, apically brown to subterminal line, veins outlined in dark brown; subterminal line an ochreous transverse shade from costa to M_1 , thence interrupted on veins to inner margin; terminal area checkered yellowish-red and dark brown, the darker color appearing on veins; terminal line brown, faint; fringes tricolor, basally ochre-

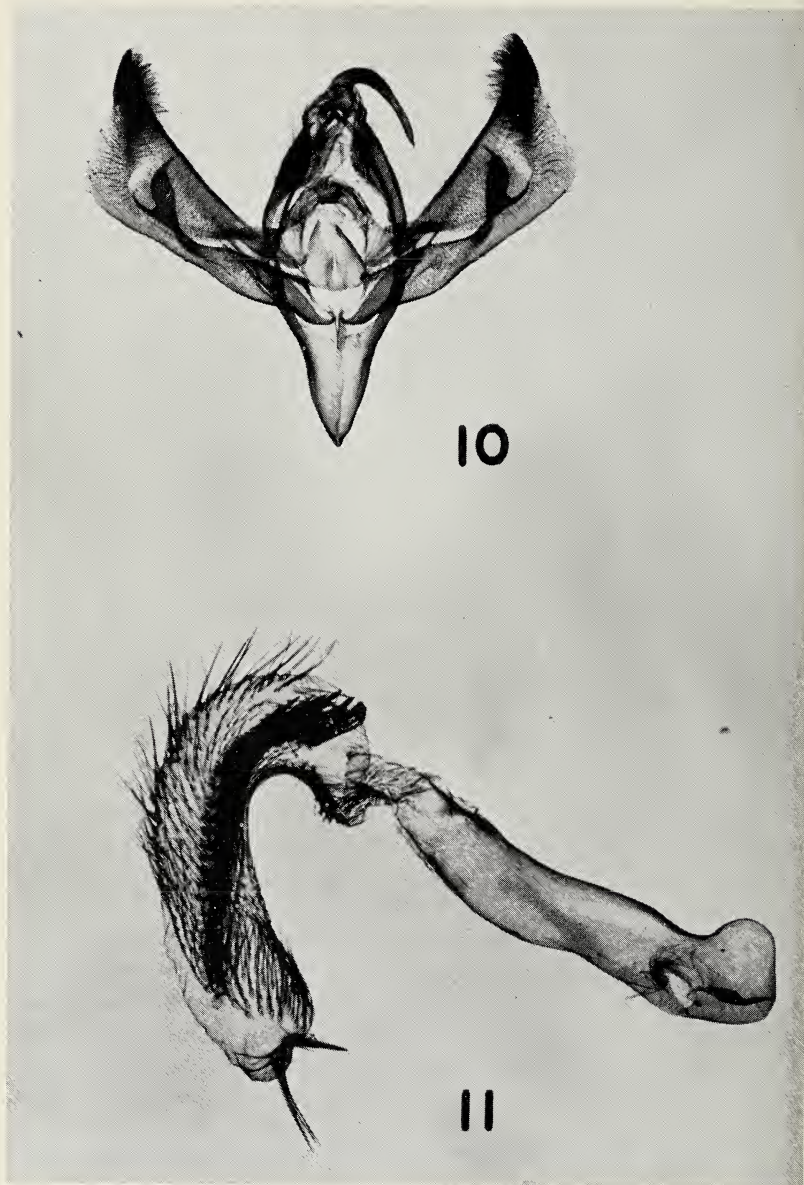


Fig. 10. Male, *O. melantho*, genitalia minus aedeagus. Road to Spencer Lakes, 8 miles southwest of Johnsville, Plumas County, California, 7 September 1960 (W. R. Bauer & J. S. Buckett), Bauer-Buckett Slide No. 66L16-3.

Fig. 11. Male, *O. melantho*, aedeagus. Data same as for fig. 10.

ous, medially dark brown, apically light brown; ventral surface ochreous basally to just preceding subterminal line, clothed in ochreous simple, elongate hairs; transverse posterior line represented costally as dark brown dash, thence only a suggestion of it appearing on medial veins; exterior border dark brown; fringes appearing tricolor, basally ochreous, somewhat darker between veins, medially dark brown, apically tan; secondaries dorsally with basal two-thirds ochreous, basal one-third scantily irrorated with brown scales, this irroration appearing concealed due to additional clothing of elongate simple ochreous hairs; faint brown scalation present just preceding exterior band on Cu_1 , Cu_2 , M_1 , and M_2 ; apical one-third of wing a dark brown band, the veins contained therein outlined in near black scales; fringes tricolor, basally ochreous, medially dark brown, apically creamy-white; ventral surface ochreous for basal three-fourths, apically with a broad brown band (otherwise marked as in dorsal surface); discal lunule faint; fringes lighter than dorsal surface, mostly ochreous, but with brown medially. Abdomen dorsally clothed in brown and ochreous scales, intermixed with sparsity of light tan simple hairs; apically clothed in admixture of brown and ochreous elongate flattened and simple hairs; ventrally clothed in tan simple scales and simple hairs. Greatest expanse of forewing 16 mm. Genitalia as in figures 8 and 9.

Female: More somber in coloration than in male, lacks as much reddish coloration as in male; primaries with more brown coloration; basal one-third of secondaries darker than in male, as though a dirty brownish coloration; ventral surface of primaries with brown in the tan basal three-fourths of surface, both median shade and transverse posterior line represented in dark brown costally, otherwise surface as in male; secondaries ventrally as in male, but with less yellow coloration, so as to appear "washed out." Greatest expanse of forewing 16 mm. Genitalia as in fig. 12. Holotype in collection of Entomology type collection, University of California, Davis, California.

Specimens examined

Holotype male: Johnsville, Plumas County, California, 6 September 1959, ex. 15 watt fluorescent black light (W. R. Bauer and J. S. Buckett). Paratypes: 64 males and 33 females; 1 female (designated Allotype) same locality and collectors as for Holotype, 8 September 1960; 1 male, same locality as holotype, 21 September 1962 (H. J. Pini), Bauer-Buckett Slide No. 66L16-1; 1 male, same locality as preceding, 10 October 1966 (H. J. P.), Bauer-Buckett Slide No. 66L19-3; 1 male, same locality as preceding, 3 October 1966 (H. J. P.), Bauer-Buckett Slide No. 66L19-1; 1 female, same locality as holotype, 15 September 1962 (H. J. P.), Bauer-Buckett Slide No. 66L16-2; 1 female, same locality as preceding, 8 October 1966 (H. J. P.), Bauer-Buckett Slide No. 66L19-2; 1 female, same locality as preceding, 3 October 1966 (H. J. P.), Bauer-Buckett Slide No. 66L19-4;

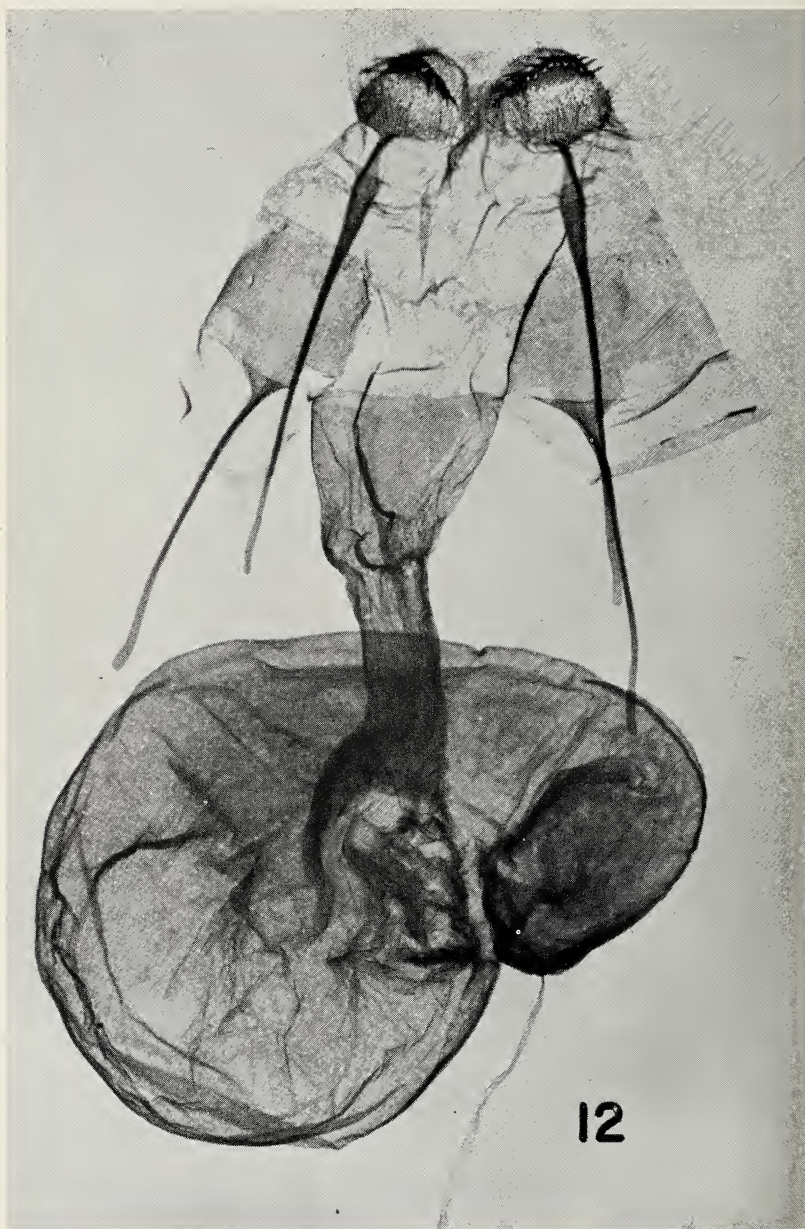


Fig. 12. Paratype female genitalia, *O. sandaraca*. Johnsville, Plumas County, California, 15 September 1962 (H. J. Pini), Bauer-Buckett Slide No. 66L16-2.



Fig. 13. Female genitalia, *O. melantho*. Mt. Ingalls, Plumas County, California, 12 September 1961 (W. R. Bauer & J. S. Buckett), Bauer-Buckett Slide No. 66L16-4.

45 males, 23 females, Johnsville, 2 September - 5 November 1959 - 1966 (H. J. P., W. R. B., J. S. B., and M. R. Gardner); 1 male, Road to Spencer Lakes, 8 miles s.w. Johnsville, Plumas County, California, 24 August 1961 (W. R. B. & J. S. B.); 5 males, 2 females, same locality as preceding, 10 September 1961 (W. R. B. & J. S. B.); 1 male, same locality as preceding, 9 September 1966 (J. S. B., M. R., R. C., J. L. & B. W. Gardner); 1 male, 1 female, same locality as preceding, 26 September 1959 (H. J. P.); 1 male, Nelson Creek, Plumas County, California, 17 September 1940 (W. R. B.); 1 male, same locality and collector as preceding, 2 September 1940; 1 male, 1 female, Monitor Pass, Alpine County, California, 8 September 1964 (W. R. B. & J. S. B.); 1 male, same locality and collectors as preceding, 9 September 1964; 3 males, Woodfords, Alpine County, California, 8 October - 21 October 1962; 1 male, Grizzly Meadows, Trinity County, California, 10 September 1964 (G. E. Buxton); 1 female, 6 miles n.w. Cedarville, Modoc County, California, 8 September 1963 (W. R. B. & J. S. B.); 1 female, Tulelake Inspection Station, Modoc County, California, 22 September 1965; 1 male, 2 females, 3 miles n. Tollgate, Umatilla Co., Oregon, 6 September 1963 (W. R. B. & J. S. B.).

Oncocnemis sandaraca can readily be distinguished from *O. melantho* by the great differences in color and lesser differences in maculation. *O. sandaraca* possesses yellowish-red to ochreous-brown primaries dorsally; whereas, *melantho* possesses greyish to greyish-olive primaries dorsally. The ventral surface of the primaries in *sandaraca* is as described, but in *melantho*, the lighter portion is off white and not at all ochreous, or possessing any yellowish color; also *melantho* may have a black transverse medial band (corresponding to the median shade of the dorsal surface) either strongly or weakly expressed; the exterior band in *melantho* is considerably broader than that of *sandaraca*. The secondaries of each species are distinctly different interspecifically. *O. sandaraca* possesses secondaries as described; whereas, dorsally *melantho* possesses a dark basal one-third, a white, or brown medial one-third and a broad black exterior band (as in figures 4 and 5); the fringes are noticeably more whitish than in *sandaraca*. The ventral surface of the secondaries in *melantho* are also quite different than for *sandaraca*: dorsally they are with basal and medial transverse areas white, or irrorated with black scales; two areas are separated by a black band; just preceding broad exterior band there is another faint black line which parallels the inner margin of this broad black band. This exterior band in *melantho* is much broader than the exterior band in *sandaraca*, and *melantho* possesses much whiter fringes in comparison to *sandaraca*.

Nothing is yet known concerning the immature stages of either species, but it would not be all too surprising to discover that larvae of both species feed on the same plant species. The genitalic slides were prepared using lignin pink stain and balsam as the mounting media.

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SPECIATION IN THE *AGATHYMUS* (Megathymidae)

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I CAN REMEMBER BACK in the past when we used to collect butterflies with a net and killing jar and then there were fifteen recognized species in two genera in the family Megathymidae. Today we have 47 species in five genera in that family and the net has long since been retired after we discovered that it was much more efficient to collect these "critters" with a fox hole pick, drain spade or sharp knife. Once when we had available a few hundred specimens of these insects the taxonomy seemed comparatively simple, and now that we have several thousand specimens available for study complications present themselves.

In making a study of speciation in the *Agathymus* we must recognize a number of species complexes that exist in that genus. They are the *neumoegeni*, *chisosensis*, *hoffmanni*, *evansi*, *aryxna*, *baueri*, *alliae*, *stephensi*, *polingi*, *mariae*, *remingtoni*, *rethon*, and *indecisa* complexes. Of these the following are very complicated and indicate a considerable amount of evolution is in progress: *neumoegeni*, *hoffmanni*, *aryxna*, *mariae*, and *remingtoni*, and it is with this group that I would like to go into with some detail.

Agathymus speciation particularly in the *mariae* complex has intrigued me for a number of reasons, one of which has been the method by which new species apparently developed during the past ages from a *mariae*-like prototype. In making a detailed study of this species complex in the United States a number of very interesting observations were encountered some of which I would like to discuss briefly. One of the first things that was noticed about *mariae* was its close association with its larval food plant *Agave Lecheguilla* Torr. During the number of

¹All my research on the Megathymidae during the past six years was made possible by the National Science Foundation through research grants G-9900 and GB-398 for which I am deeply grateful.

years that I have collected *mariae* and other related species I have never found a specimen in any other species of *Agave* other than members of the *lecheguilla* complex, with the possible exception of a Mexican species that feeds in *Agave falcata* Engelm. Indications are that at one time *lecheguilla* occurred extensively from the Edwards Plateau in Texas over into New Mexico and well down into Mexico. Fossil seeds have been found in areas of Texas now completely devoid of these plants. In this vast expanse a prototype of our modern species was well established with a gene pool common to all areas. Conditions arose resulting in the eradication of *lecheguilla* plants in many sections of this great area thus disrupting the gene pool. During the many years that followed mutations occurred in the restricted populations resulting in the production of individuals that differed from the original species. These isolated populations gradually changed both biologically and morphologically into five separate species in the Texas area. *Mariae* was the first described in this complex and it was found at El Paso, in the Franklin Mountains, and for many years was considered to be the only species present all over southwestern Texas. After carefully studying specimens from 32 locations in Texas and New Mexico it was found that there was actually five different species going under the name of *mariae*. *Chinatiensis* Freeman, in the Chinati Mountains and near vicinity; *lajitaensis* Freeman, in the Lajita region of the Big Bend; *rindgei* Freeman, and *gilberti* Freeman, in the general vicinity of Del Rio; and *mariae* (B. & B.), from the Big Bend and McCamey regions westward and north to Carlsbad, New Mexico and El Paso, Texas. In no area do more than two of these species occur together and when this happens it was found that they have changed somewhat their larval feeding habits. In the Boquillas Canyon, Dryden, and Langtry areas where *gilberti* and *mariae* fly together, *gilberti* larvae penetrate into the caudex of the plant to a depth of 20 mm, whereas *mariae* does not penetrate more than 5 mm into the caudex, but does most of its feeding in the lower portion of the leaves. In the Del Rio, Juno, and Bracketville areas where *gilberti* and *rindgei* fly together *gilberti* penetrates sometimes to a depth of 30 mm into the caudex, whereas *rindgei* seldom penetrates below 20 mm. It is not unusual to find these two species and *estelleae* (Stallings & Turner) feeding in the same plant, each with a somewhat different feeding level, with *estelleae* feeding only in the leaves, *rindgei* the base of the leaves and upper caudex, and *gilberti* in the lower base of the leaves and deeper into the caudex. A rea-

sonable explanation for this is the rapidly declining population of *lecheguilla* plants in this general area, thus resulting in greater competition for food among these insects. The pH of the soil has considerable bearing on the occurrence of these species in a given habitat. *Mariae* is associated with distinctly alkaline soil, often from 7.7-8 pH; *chinatiensis* and *lajitaensis*, with soil somewhat less alkaline, around pH 7.2-7.4; and *gilberti* and *rindgei*, in soil that is neutral or only slightly alkaline, pH 7-7.1.

An interesting observation was made concerning the feeding habits of the larvae of *Aegiale hesperiaris* (Walker) and *Agathymus hoffmanni* (Freeman) in *Agave americana* L. in Mexico. In areas where *hoffmanni* is fairly abundant, especially in the valley of Mexico, the larvae feed in a small species of a parryi-like *Agave*, and overlook the larger *americana* plants, in which the larvae of *hesperiaris* are found. The *hoffmanni* trap doors are located on the lower surface and usually near the center of the leaf. In areas where both species are found in the same plant, some member of the *americana* complex, *hoffmanni* prefer the hip of the leaf for their feeding area leaving the center portion for the much larger *hesperiaris* larvae, or else the *hesperiaris* forced them into that position. Specimens of *hoffmanni* from these areas are atypical, indicating that they have evolved or else are in the process of evolving into a separate species. Both biological and morphological work on these specimens is difficult due to the scarcity of the individuals. When sufficient material is present for study it may then be possible to determine the exact status of these *hoffmanni*-like specimens.

In Arizona some parallel evolution appears to be present in various populations of *Agathymus aryxna* (Dyar). In the general area of the Chiricahua Mountains southward through Ramsey Canyon or into northern Mexico is found one population with similar characteristics. Another population begins near Globe and extends through Santa Catalina, Rincon, and Santa Rita Mountains southward through the Patagonia Mountains into Sonora, Mexico. The third is a rather variable population that occurs in the Baboquivari Mountains and possibly on southward into Mexico. Indications are that at one time this entire area was covered with a *palmeri*-like *Agave* in which fed an *aryxna*-like prototype of our modern species. Environmental conditions plus man made factors eliminated the *Agave* in large areas thus producing desert and mountain islands where the plants are still undisturbed. Individuals from each population may be recognized by the width of the spots on both wings.

Starting with the eastern population, the spots are generally separate and fairly small. In the central population, the spots are somewhat larger and tend to be closer together. While in the western population, the spots are the largest, tending to fuse together in some cases. To me there seems no doubt that we are seeing evolved three separate subspecies that eventually will assume specific status within a number of years.

In the *neumoegeni* complex we have a number of so called species that exhibit characteristics indicating a common ancestor. Possibly some of these have evolved farther than others and are specific, however others may still be in the process of changing from distinct subspecies into full species. The test of breeding has just started to be worked upon by Stallings, Turner & Stallings and the results will likely be very conclusive in forming our conception of this complex. I have collected larvae of wild hybrids of a cross between male *mariae* and female *judithae* (Stallings & Turner), as well as the same in a cross between male *mariae* and female *diabloensis* Freeman and the resulting F_1 did not resemble each other as much as the pure *judithae* and *diabloensis* do, especially the females. In all of the wild hybrids that I have seen to date involving *mariae* with some species of the *neumoegeni* complex it has always been the males of *mariae* that have resulted in the hybrids. This is based on the presence of the larvae in species of *Agave* other than members of the *lecheguilla* complex. From all evidence presented these F_1 are sterile.

Two members of the *neumoegeni* complex are associated with juvenile plants, *neumoegeni* (Edwards) and *florenceae* (Stallings & Turner). All other species are associated with mature plants running from small to large in size. *Florenceae* and *neumoegeni* morphologically resemble each other more closely than do any of the other species in this group even though there is a great distance separating them in their distribution. Genetically speaking the entire complex is closely related.

In the *remingtoni* complex we have three described species, *remingtoni* (Stallings & Turner), *estelleae* (Stallings & Turner) and *comstocki* (Harbison), and several undescribed species. Genetically they are related, biologically they are very different. *Remingtoni* is found in the mountains in very rugged terrain, often on cliffs, with the pH on the acid side, and feeding upon a member of the *lecheguilla* complex. *Estelleae* is associated with alkaline or near neutral soil, usually in the plains country or else

where it is slightly hilly, and feeding upon another member of the *lecheguilla* complex. *Comstocki* is found in hilly, desert, areas of Baja California (pH has not been checked), feeding upon *Agave shawii* Engelm., which is not at all related to *lecheguilla*. The general range of *remingtoni* is Victoria, Tamps., Mexico southward to the Jacala, Hidalgo, area, while *estelleae* occurs north and west of Victoria. All indications point to a common ancestor of these two species that occurred in an area where the gene pool was available for all regions of the range. Due to environmental changes, both man made and natural, the gene pool was disrupted, eventually resulting in the formation of separate subspecies and eventually species.

In conclusion I would say that in the genus *Agathymus* we have had three major prototype complexes, the *neumoegeni*, *aryxna*, and *mariae*, and from these three all of our present day species evolved.

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THE EGGS AND FIRST INSTAR LARVAE OF THREE CALIFORNIA MOTHS

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IN REARING LEPIDOPTERA from captured females of identified species it occurs not infrequently that foodplants and early stages have not previously been recorded, and the rearing ends with the newly emerged larvae because of their refusal to accept experimentally offered plants.

It is justifiable to publish such incomplete records for the purpose of encouraging other entomologists, located in areas of varying plant associations to carry on the experiments with plants not available to the original recorder.

Three examples of such incomplete records are here included:

Scotogramma defessa Grote

Eggs were secured from a gravid female during the second week in April, 1962, at Del Mar, California. They hatched April 20, '62.

EGG: (Figure 1, No. 1), hemispherical, the base flattened and the top evenly rounded. It is topped by a minute round micropyle with a raised center and a surrounding depressed circlet. The ground color is a light straw. The basal diameter is approximately 0.65 mm. and the height 0.4 mm. The surface is covered by 48 vertical ribs, many of which coalesce as they approach the curved top. From 12 to 15 of these extend across the depressed circlet and about on the micropyle. The raised vertical ribs are topped by minute glistening pearly-white nodules.

Higher magnification discloses low horizontal ridges or lines running across the troughs between the vertical ridges.

The illustration shows the egg on lateral aspect, tipped slightly forward to show the micropyle.

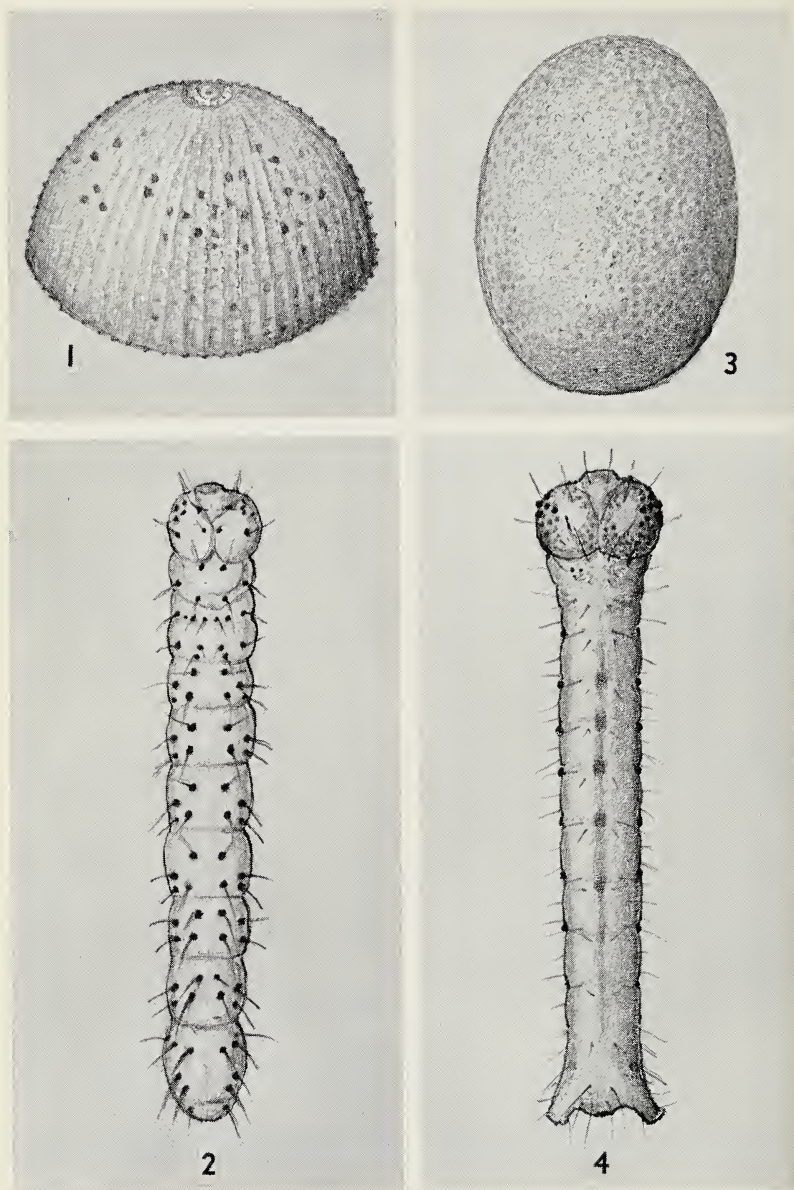


FIGURE 1

- No. 1. Egg of *Scotogramma defessa*, lateral aspect, X 50.
No. 2. First instar larva of *S. defessa*, X 45.
No. 3. Egg of *Campptogramma neomexicana* X approximately 70.
No. 4. First instar larva of *C. neomexicana* X approx. 38.

FIRST INSTAR LARVA: (Figure 1, No. 2.), Body, cylindrical, translucent and white. Length, 2. to 2.25 mm. The head is yellow, and wider than the first segment. Numerous setae are scattered over the body. These are black, and arise from black papillae. Those on the thoracic segments are in line transversely across each segment. On the typical abdominal segments they alternate in a zig-zag pattern, giving the impression of two transverse rows running along each segment. There are two pairs of prolegs in addition to the anal pair.

No food plant notes were available. I tried lettuce, clover, parsley, sage, yarrow, oak, willow, *Ceanothus* sp., *Eriogonum* sp., *Adenostoma* sp., *Artemisia* sp., *Oenothera* sp., *Mimulus* sp., and *Rhus* of three separate species, without avail.

Camptogramma neomexicana Hulst

A captive female laid numerous eggs April 24, 1962. They were deposited singly on their sides.

EGG: (Figure 1, No. 3.), oval; ground color a delicate pink, but appearing nearly white because of the reticulation of raised white walls outlining hexagonal cells. Length of egg, 0.75 mm. Width, 0.4 mm. Just before hatching the eggs lose some of their pink tinge and become spotted with light chrome. Hatching occurred May 3, 1962.

FIRST INSTAR LARVA: (Figure 1, No. 4.), Length, 2.5 mm. Head width approximately 4.35 mm., broader than first segment and somewhat flattened; dull yellow with a darker tinge on the outer edges of cheeks and many bulging prominent black ocelli. Apparently there are six on each cheek, but they are somewhat confused with numerous black spots in the near vicinity. These spots occur along the frontal and adfrontal sutures and on the sides of the cheeks.

The body color is yellow. From the 4th to about the 10th segment there is a longitudinal middorsal stripe, discontinuous in some examples and more conspicuous in others. This line has a darker shading on the segmental junctures. There are raised black spots or papillae running in line longitudinally on the spiracular area, one on each segmental juncture. The legs are yellow as are also the anal prolegs and single pair of prolegs.

The setae are predominantly white.

The young larvae were tested on honeysuckle, oak, willow, bur clover, chamise, sage, toyon, pine, cyprus, and *Rhus* of three species, all without success.

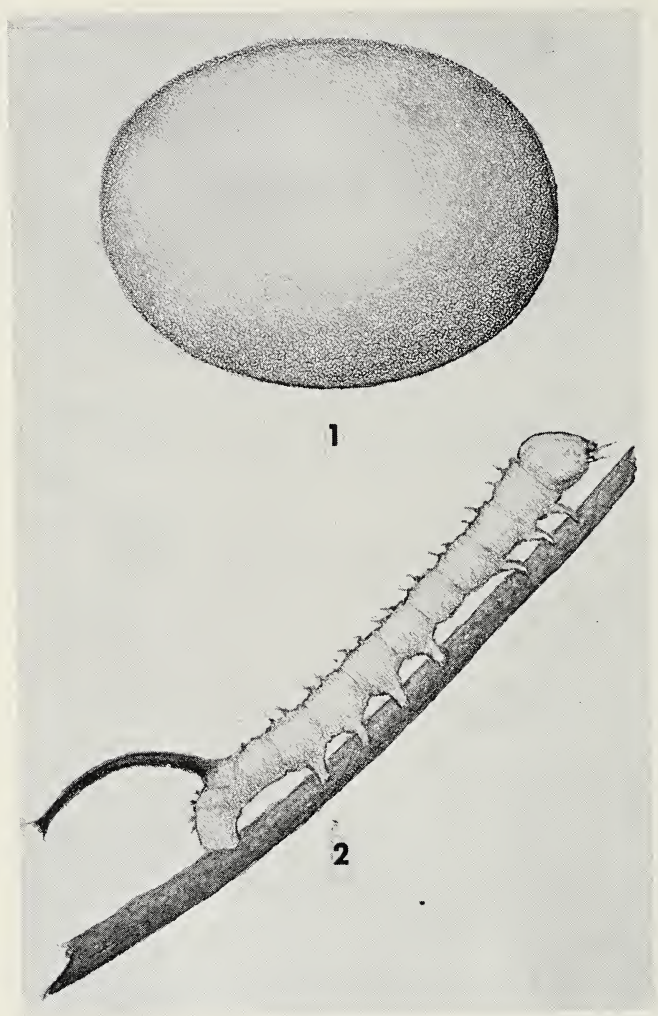


FIGURE 2

No. 1. Egg of *Sphinx vashti* X 45.No. 2. First instar larva of *S. vashti* X 15.

THE EGG AND FIRST LARVAL INSTAR OF
Sphinx vashti Strecker

Eggs of the rare hawk moth, *Sphinx vashti*, were sent me September 20, 1955 by Frank Sala. They were obtained September 13, '55 from a confined female collected at Wheaton Springs, Mescal Range, San Bernardino County, California.

EGG: (Figure 2, No. 1), length 1.8 mm., by 1.2 mm. tall. Color, a delicate green. The surface is smooth, and there is apparently no reticulated pattern or network of cell impressions.

The eggs hatched September 21, 1955.

FIRST INSTAR LARVA: (Figure 2, No. 2), length, 5 mm., not including the caudal horn. The latter measures 2.55 mm.

Head: larger than first segment; translucent light green including the ocelli and all appendages. Later the ocelli and tips of the mandibles show a tinge of gray.

Body: cylindrical, tapering gradually toward the cauda, but slightly expanded at the 11th segment where there is a large caudal horn. This is recurved caudally, and ends in a bifurcated tip. It is brownish-black in color.

The legs and prolegs are concolorous with the light green body.

I was unable to find a food plant that the larvae would accept, and they all died shortly after the accompanying notes and illustrations were made.

AN ADDITIONAL FOOD PLANT RECORD FOR
Papilio thoas autocles R. & J.

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In Holland's revised edition of the "Butterfly Book", 1931, p. 317, he lists the genera *Ptelea*, *Xanthoxylon*, and the various species of *Citrus* which have been introduced into America, as the food plants of *Papilio thoas autocles*.

As a result of rearing this butterfly in Puerto Vallarta, Mexico, during the summer of 1957, as recorded in "Estudios de los Ciclos Biologicos en Lepidopteros Mexicanos", authored in cooperation with Dr. Leonila Vazquez Garcia, and run in the Anales del Instituto de Biologia, Vol. 31, 1961, we were able to add the genus *Piper* to the list of host plants.

An additional food plant for this butterfly was collected at the time, but proved puzzling to the cooperating botanists.

This month (August, 1963) I received word from Dr. Reid Moran, botanist of the San Diego Museum of Natural History that a determination of the unknown plant has finally been made.

He states that "it is *Monnieria trifolia* L., very rarely collected in Mexico and overlooked in the North American Flora; also omitted from Trees and Shrubs of Mexico, though perhaps because not considered a shrub.

Accordingly, we can now list *Monnieria trifolia* L., as another food plant of *Papilio thoas autocles*.

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A NEW SPECIES OF *POLIA* OCHSENHEIMER

FROM CALIFORNIA AND NOTES ON *POLIA DISCALIS* (GROTE)
(NOCTUIDAE:HADENINAE)

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POLIA PINIAE BUCKETT AND BAUER, new species, has long been masquerading under the name *P. discalis* (Grote), and until recently this error has gone unnoticed. While working over this section of the genus *Polia*, the authors recognized a confused situation, and with concentrated effort and further research, it was agreed that there were at least two species under the name *discalis*. We also have a large series of *P. discalis* from the eastern Sierra Nevada of California which is perhaps of subspecific rank, but at the present time it is felt best to retain this series as merely a light colored form of *discalis*.

POLIA PINIAE Buckett and Bauer, new species

Male: Ground color of primaries a whitish grey, transverse lines hardly discernable. Head with vertex and frons clothed predominantly in whitish flattened hairs, but with some dark brown flattened hairs intermingled; frons smooth, broadly truncately rounded; palpi clothed exterolaterally with whitish flattened hairs, but predominantly with brown and dark brown elongate, flattened hairs; antennae appearing dorso-ventrally bicolor under 10X power, with scape and pedicle clothed in brown and white intermixed elongate scales; flagellomeres with small fasciculate hairs ventrally, dorsally clothed in whitish and brownish scales; compound eyes moderately to heavily haired; latrad of eyes, a bunch of black fine hairs forms a dense cluster. Thorax with collar composed of flattened hairs and elongate scales, basally whitish, medially black (so as to form a conspicuous transverse bar), apically white tipped; dorsally clothed in silvery-whitish elongate scales, some brown elongate scales intermixed also; anterior tuft composed of predominantly dark brown flattened, dentate scales, some whitish scales of same type intermixed; posteriorly from anterior tuft a thin brown line of flattened hairs leads to suggestion of diminutive divided posterior tuft; patagia exterolaterally composed of dark brown fine silken hairs; legs with pro and meso femora dorsally clothed in brown, metafemora clothed dorsally in dirty whitish colored scales; all legs with tibiae clothed in mixture of whitish and brown scales; tarsi clothed dorsobasally in dark brown

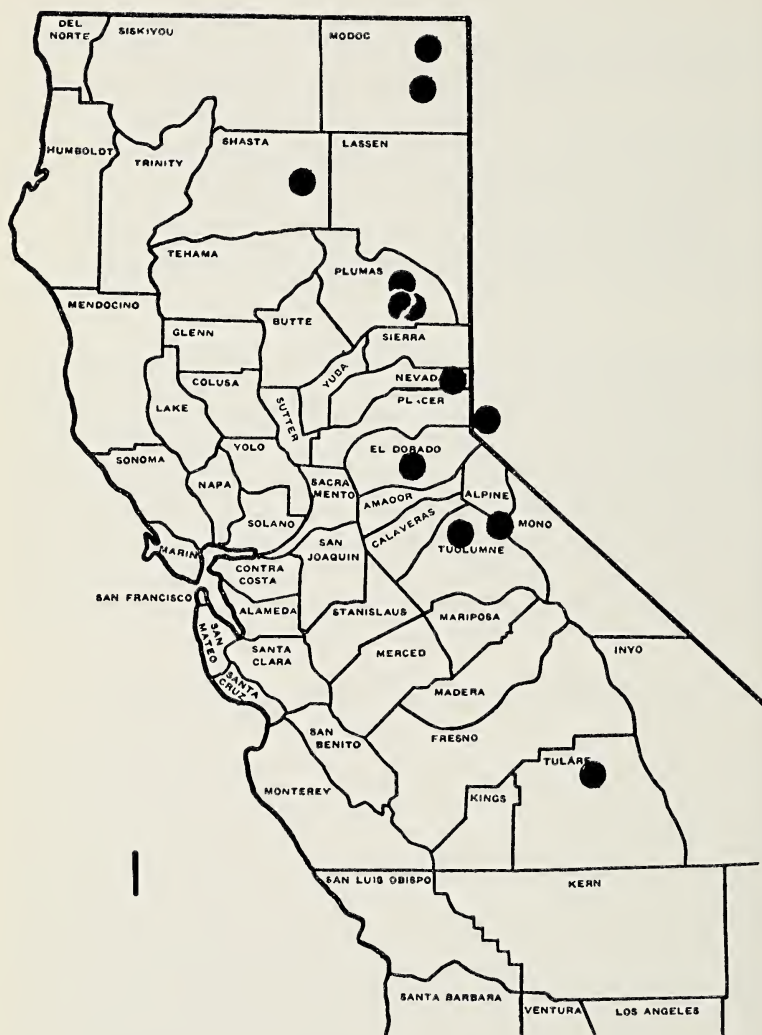


Fig. 1. Distribution map indicating the presently known distribution of *Polia piniae* Buckett and Bauer.

scales, dorso-apically and ventrally clothed in whitish scales; unguis moderately interolaterally bifid; primaries dorsally clothed in ground color, sparsely irrorated with fuscous scales (which gives a light ashey grey, or greyish white appearance); basal line present as thin black apically pointed "V" on costa, thence wanting, or hardly discernable; basal and transverse anterior areas of ground color, contiguous; transverse anterior line present on costa as is basal line, but broader and geminate costally, thence diminishing into a faint transverse line to inner margin, hardly discernable; median area with very slightly darker shade than ground color; orbicular very broad, subquadrangular, open on costal margin, outlined faintly in black, filled with ground color; area between orbicular and reniform irrorated with blackish scales, less than width of orbicular; reniform large, color as in orbicular, nearly contiguous with orbicular on Cu₁; transverse posterior line represented as dark shade on costa, thence almost entirely obliterated; subterminal space of ground color; subterminal line strongly represented costally, opposite of discal area and in tornus area (as in figure 2); tornus area with blackish bilobed mark, lobes terminally directed; terminal space of ground color; terminal line faint, represented by blackish lunules between veins; fringes basally whitish, thence of intermixed brown and whitish spatulate scales; ventral surface with costal edge and outer margin silvery-grey; central portion of wing fuscous; veins outlined in deep smokey fuscous; transverse posterior line represented costally as dark dash; secondaries dorsally light ochreous brown, basally and terminally darker than lighter median band; veins outlined in smokey; discal lunule faint, dark brown; terminal line dark brown; fringes tricolor, basally ochreous, medially brown, apically white tipped; ventral surface whitish, veins faintly outlined in fuscous; discal lunule faint; remainder of surface as in dorsal surface. Abdomen dorsally whitish; mid dorsal hairs blackish, almost appearing tuft-like; posteriorly whitish hairs and scales intermixed with dark brown; ventrally clothed in whitish hairs. Greatest expanse of forewing 25 mm. Genitalia as in figures 6 and 9.

Female: As in male except antennae lacking fasciculations as in male, but rather possessing fine ciliations; primaries and secondaries slightly darker than in male. Abdomen as in male except slightly darker dorsally. Greatest expanse of forewing 26 mm. Genitalia as in figure 4.

SPECIMENS EXAMINED

HOLOTYPE male: Johnsville, Plumas County, California, 5 July 1962 (Helena J. Pini). Paratypes: all specimens from California unless otherwise stated; 175 males, 39 females; 1 female (designated Allotype), same locality as Holotype, 3 July 1959 (W. R. Bauer and J. S. Buckett); 1 male, *Johnsville*, Plumas Co., 24 July 1955 (W. R. B. & J. S. B.), Bauer-Buckett slide No. 66L2-3; 1 male, 6 July 1962 (H. J. Pini), Bauer-Buckett slide No. 64D26-4; 1 female, 5 August 1962 (H. J. P.), Bauer-Buckett slide No. 66L6-5; 1 female, 10 August 1962 (H. J. P.), Bauer-Buckett slide No. 66L7-2; four males, 1 female, 5 August 1962 (H. J. P.); 1 female, 20 August 1962 (H. J. P.); 1 female, 1 August 1962 (H. J. P.); 14 males, 8 females, 7 August 1962 (H. J. P.); 6 males, 2 females, 9 August 1964 (H. J. P.); 1 female, 11 August 1965 (H. J. P.); 1 male, 21 July 1965 (W. R. B. & J. S. B.); 3 males, 6 July 1965 (H. J. P.); 10 males, 1 female, 24 July 1965 (H. J. P.); 1 male, 27 July 1964 (H. J. P.); 1 male, 21 July 1964 (H. J. P.); 1 male, 13 July 1964 (H. J. P.); 1 male, 16 July 1964 (H. J. P.); 2 males, 24 July 1964 (H. J. P.); 2 males 17 July 1964 (H. J. P.); 1 male, 12 July 1964 (H. J. P.); 1 female, 26 July 1965 (H. J. P.); 13 males, 2 females, 17 July 1964 (H. J. P.); 3 males, 16 July 1964 (H. J. P.); 3 males, 13 July 1964 (H. J. P.); 4 males,



Fig. 2. Holotype male, *Polia piniae*. Johnsville, Plumas Co., California, 5 July 1962 (Helena J. Pini).

Fig. 3. Allotype female, *Polia piniae*. Johnsville, Plumas Co., California, 3 July 1959 (W. R. Bauer and J. S. Buckett).

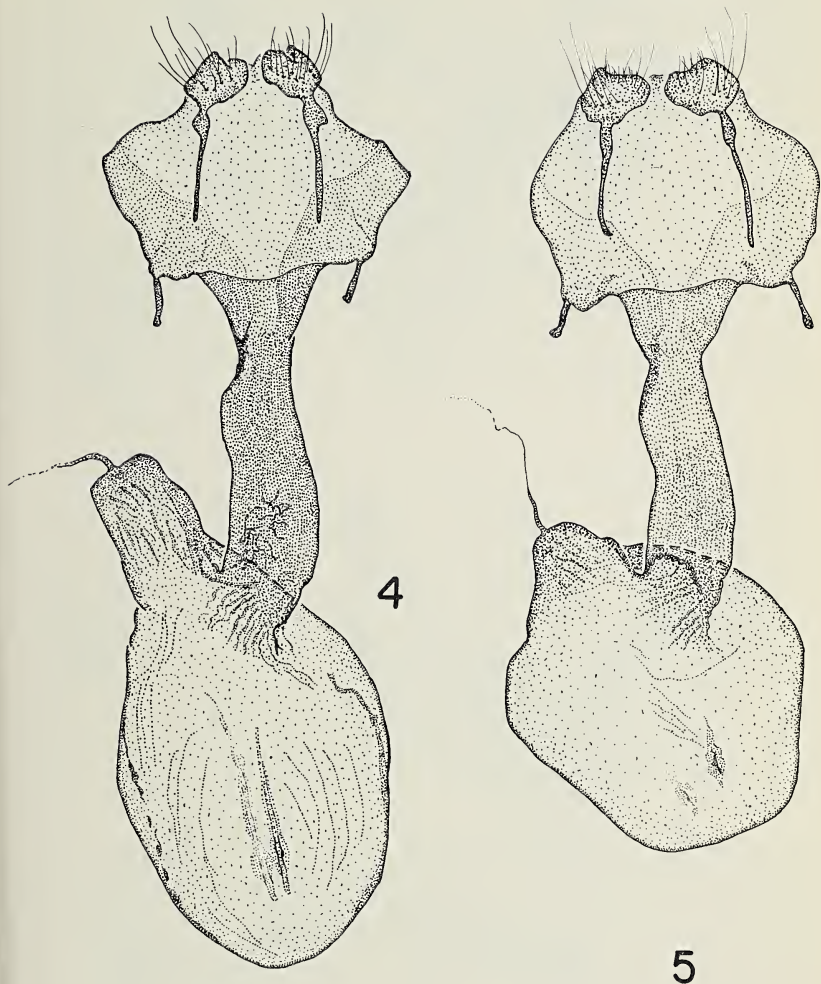


Fig. 4. Paratype female. Genitalia of *Polia piniae*. Johnsville, Plumas Co., 10 August 1962 (H. J. Pini), Bauer-Buckett slide No. 66L7-2.

Fig. 5. Female genitalia of *Polia discalis* (Grote). Rabbit Ears Mountains, 10 miles southeast of Steamboat Springs, Routt Co., Colorado, elevation 8200', 28 July 1962 (J. S. Buckett and G. M. Trenam), Bauer-Buckett slide No. 66L7-1.

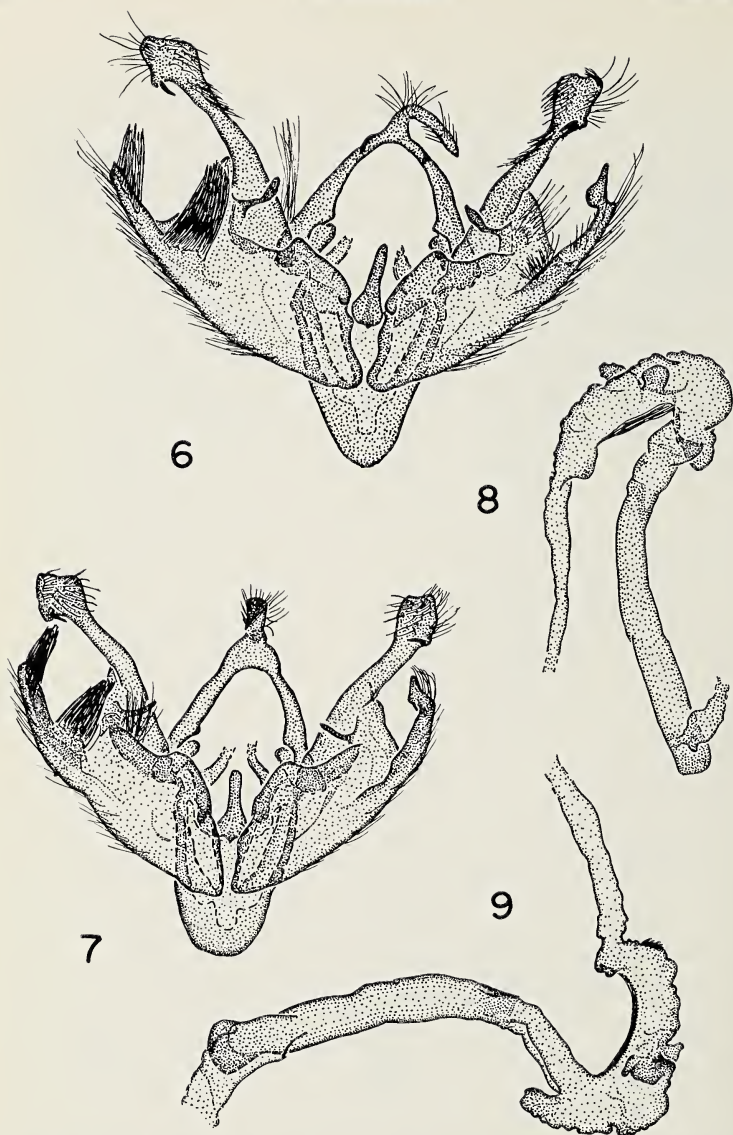


Fig. 6. Paratype male. Genitalia minus aedeagus of *Polia piniae*. Johnsville, Plumas Co., 24 July 1955 (W. R. Bauer and J. S. Buckett), Bauer-Buckett slide No. 66L2-3.

Fig. 7. Male genitalia minus aedeagus of *Polia discalis*. Data same as for figure 5, except for slide No. which is: Bauer-Buckett slide No. 66L2-1.

Fig. 8. Aedeagus of *Polia discalis*. Data same as that for fig. 7.

Fig. 9. Aedeagus for *Polia piniae*. Data same as that for fig. 6.

7 July 1965 (H. J. P.); 1 male, 9 September 1963 (H. J. P.); 2 males, 6 July 1965 (H. J. P.); 1 male, 1 female, 21 July 1964 (H. J. P.); 12 males, 2 females, 19-23 July 1964 (H. J. P.); 6 males, 2 females, 27 July 1964 (H. J. P.); 1 male, 17 July 1962 (H. J. P.); 3 males, 1 female, 11 July 1962 (H. J. P.); 21 males, 1 July 1965 (H. J. P.); 3 males, *Mohawk*, Plumas Co., 4-7 July 1946 (W. R. Bauer); 1 female, 12 July 1946 (W. R. B.); 3 males, *Mt. Ingalls*, Plumas Co., 11 July 1964 (W. R. B., J. S. B., M. R. Gardner); 4 males, 1 female, *Pinecrest*, Tuolumne Co., 25 July 1965 (Robert Mason); 14 males, 1 female, 9 July 1965 (R. M.); 11 males, 16 July 1965 (R. M.); 1 male, 2 July 1965 (R. M.); 1 male, 2 miles west, *Sonora Pass*, Tuolumne Co., 1 July 1966 (G. M. Buxton); 3 males, *Wentworth Springs*, El Dorado Co., 8 July 1961 (W. E. Simonds); 1 male, *Donner Lake*, Nevada Co., 20 July 1962 (G. M. B.); 3 males, *Carnelian Bay*, Placer Co., 12 July 1965 (F. D. Parker); 3 males, 4 females, *Manzanita Lake*, Shasta Co., 13 August 1963 (G. M. Buxton); 1 male, *Hat Creek*, Shasta Co., 26 July 1964 (R. R. Pinger); 1 male, *Cedar Pass*, 6 miles northwest of Cedarville, Modoc Co., 4 July 1962 (W. R. B., J. S. B., G. M. Trenam); 1 female, *Lassen Creek*, north of Davis Creek, Modoc Co., 28 July 1957 (W. R. B. & J. S. B.); 1 male, *Mineral King*, Tulare Co., 19 July 1963 (W. E. S.); 1 male, 1 female, *Zeypher Cove*, Douglas Co., Nevada, 20 August 1963 (Bobbie Ellis); 1 male, 27 August 1963 (B. E.).

The Holotype is deposited in the Entomology Type Collection, Department of Entomology, University of California, Davis, California. The female Allotype and paratypes are deposited in the private collection of the authors. Other paratypes will be deposited in the following institutions and collections: American Museum of Natural History, New York; California Academy of Sciences, San Francisco; California State Department of Agriculture, Sacramento; Canadian National Collection, Ottawa, Ontario; J. G. Franclemont collection, Ithaca, New York; Los Angeles County Museum of Natural History; United States National Museum, Washington, D. C.; University of California, Berkeley and Davis.

Polia piniae can be readily distinguished from *P. discalis* by the former possessing sparsely fuscous irrorated primaries, therefore appearing ashey-grey, or silvery-grey; whereas, *discalis* possesses primaries that are thickly and evenly irrorated with fuscous, therefore appearing darker or bluish grey. The space between the orbicular and reniform is less than the width of the orbicular in *piniae*; whereas, in *discalis* this same space is as wide as the orbicular or wider in some specimens. Both the male and the female genitalia of *piniae* are specifically distinct from the genitalia of *discalis* also (as can be seen in figures 4-9).

P. piniae is apparently a mid to late summer flier, predominantly at moderate elevations in the Sierra Nevada of California and elsewhere it occurs. The light form of *discalis* occurs on the

eastern edge of the Sierras where there is considerable influence from Great Basin type flora; whereas, typical *discalis* occurs at higher elevations in the Rocky Mountainous regions of the central United States, and more specifically in Colorado. To date nothing is known concerning the immature sages of *piniae*.

We take great pleasure in naming this species in honor of the ardent collector and naturalist, Mrs. Helena J. Pini of Johnsville, California. The genitalic illustrations were prepared by the first author.

KNOW YOUR AUTHOR

BRIAN OLIVER CORDERY GARDINER

Born: Ealing, England, March 10, 1923.

St. Bartholomews Hospital Medical School, first M. B.

Married in 1951, 3 boys.

Positions: Left St. Bartholomews due to war, after which worked for a short time in the Entomology Department, British Museum (Natural History). Transferred to present position on Agricultural Research Council.

Interests: The lepidoptera of Cambridgeshire, especially the fenland area; Pieris brassicae, its varieties, races and virus disease; breeding the Saturniidae of the world, and breeding lepidoptera out-of-season and on artificial diets.

Publications: About 75 notes and articles on lepidoptera, mostly in British journals.



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A GYNANDROMORPH OF
LYCAENA GORGON

PAUL A. OPLER

1131 E. 10th St.
Albany, California



Fig. 1. A gynandromorph of *Lycaena gorgon* collection data: Castle Rock Park, Mt. Diablo, Contra Costa County, California, May 10, 1953. Collected by Paul A. Opler.

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THE DISTRIBUTION AND BIONOMICS OF ARCTIC-ALPINE *LYCAENA PHLAEAS* SUBSPECIES

IN NORTH AMERICA

OAKLEY SHIELDS

5151 Alzada Drive, La Mesa, California

and

JOHNSON C. MONTGOMERY

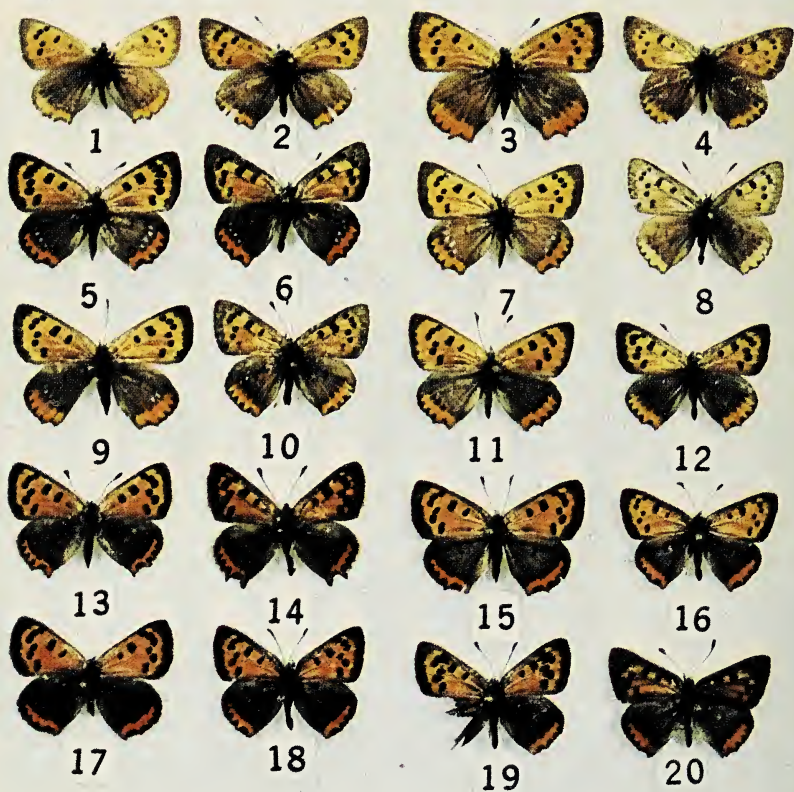
3660 Altamont Way, Redwood City, California

INTRODUCTION

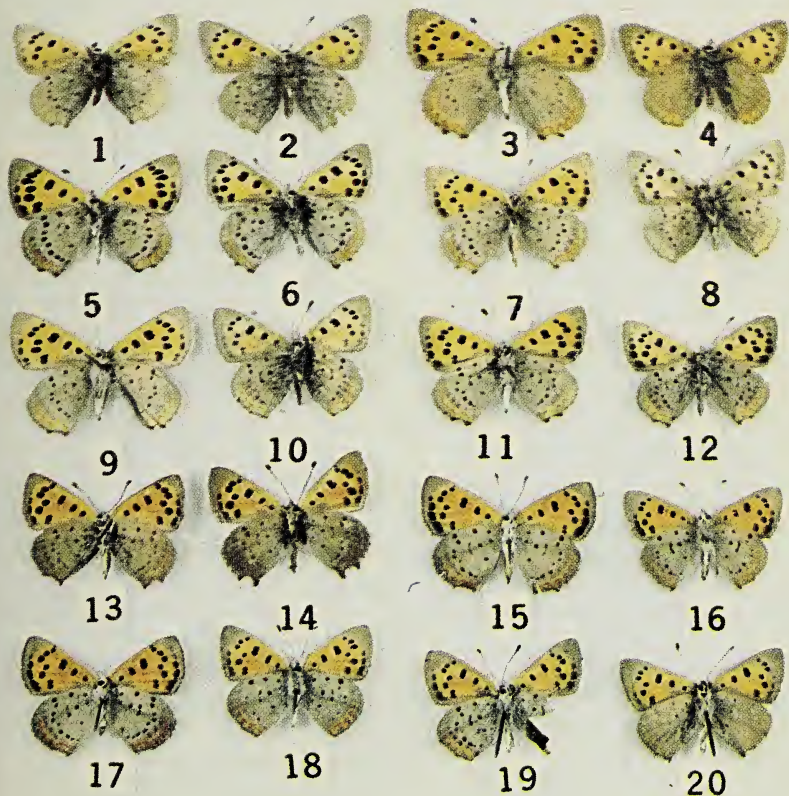
FORD (1923) DEFINES THE RANGE of *Lycaena phlaeas* (Linnaeus) and its subspecies as "throughout the greater part of the Northern Hemisphere," including most of the Palaearctic and Nearctic Regions and part of the Oriental and Ethiopian Regions. The species is subject to remarkable seasonal, geographical, and individual variation within this range (Ford, 1923). In spite of this variation, the haploid chromosome number for three subspecies of *L. phlaeas* from Japan, Finland, and the United States is 24 (Maeki & Remington, 1960), strongly indicating a stable chromosome number for the species throughout its range. Lees (1963) has shown that a changed environment can radically alter the phenotype of *phlaeas*.

TYPE LOCALITIES

Linnaeus (1761) described *L. phlaeas* from "in pratis Westmanniae." Westmannia is located in Sweden (Tite, 1957). Boissduval (1852) described *L. p. hypophlaeas* from "Nord de la Californie. Il se retrouve dans tout le nord des Etats-Unis." This translates, "North of California. It is found in all the northern United States" (Dod, 1907). Thus the type locality is not "California" as listed by Klots (1951) and Comstock & Huntington (1960) and alluded to by Forbes (1960) and Garth & Tilden (1963). We do not know of a precise locality for *hypophlaeas* nor where the type specimen(s) is located. (California material



Figs. 1 and 2. *Lycaena phlaeas feildeni*, 1, 2; *phlaeas* ssp., 3-10; *p. "hypophlaeas,"* 11, 12; *phlaeas*, 13, 14; *p. americana*, 15-18; *p. americana* f. *fasciata*, 19; *p. arethusa*, 20. 1. & 2. Clyde Inlet, Baffin Id., N.W.T. (BMNH), ♀, ♂. 3. & 4. McKinley Park, Alaska (AMNH), ♀, ♂. 5. & 6. ½ mi. W. Halfmoon Park, Crazy Mtns., Sweet Grass Co., Montana, ♀, ♂. 7. & 8. Bear Tooth Mtns., Carbon Co., Montana (AMNH), ♀,



♂ . 9. Amphitheater Lake, 10,000', Grand Tetons, Wyoming (CU), ♀ .
 10. Beartooth Lake, Wyoming (CU), ♂ . 11. & 12. N. slope Mt. Dana,
 11,000-12,000', Mono Co., California, ♀ , ♂ . 13. & 14. Uddevalla, Swe-
 den (BMNH), ♀ , ♂ . 15. & 16. Near Prairie Village, Johnson Co., Kan-
 sas, ♀ , ♂ . 17., 18., & 19. Camp Lucerne, Waushara Co., Wisconsin, ♀ , ♂ ,
 ♂ . 20. Plateau Mt. 8200', Alberta, ♂ .



Fig. 3. Map of the North American *Lycaena phlaeas* subspecies distribution (excluding *americana*). Localities indicated by black dots. Shaded portion is the distribution of *Oxyria digyna* as figured by Mooney & Billings (1961) and Billings (in litt.).



Fig. 4. Variation of "*hypophlaeas*" series from N. slope Mt. Dana, Mono Co., California. Left half females, right half males.

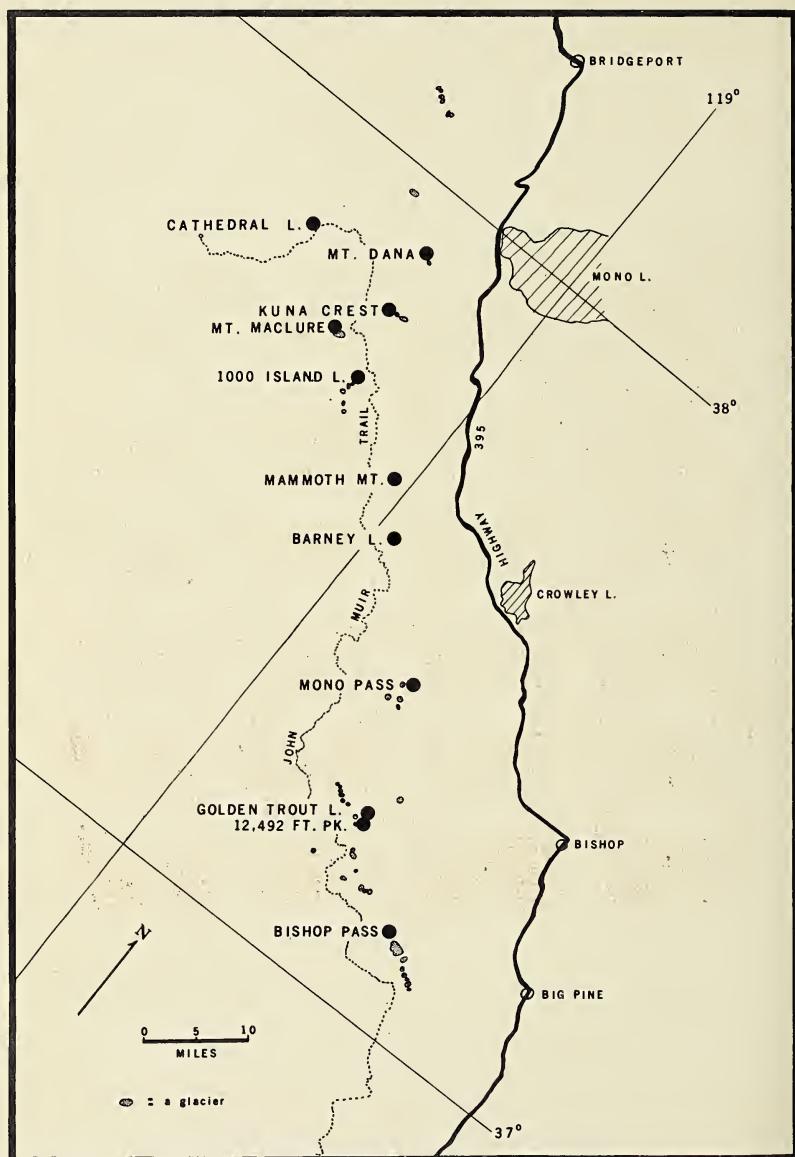


Fig. 5. Map showing the distribution of "*hypophlaeas*" in the Sierra Nevada Mtns., California. Localities indicated by black dots. Map adapted from Starr (1956).

will be referred to as "*hypophlaeas*" in this paper as a matter of convenience.) M'Lachlan (1878) described *L. p. feildeni* from two males and one female from "Lat. $81^{\circ} 45'$." The British Museum of Natural History contains these three specimens which bear the label, "Grinnell Land, west side of Smith Sound, Arctic America. 78-83 Lat. (81-45) Capt. Feilden R. N. 77-101." (Tite, in litt.). These were collected in 1875 or 1876 (Wolff, 1964). Dod (1907) described *arethusa* from five males and eight females: one male from ca. 35 mi. SW Calgary, Alberta (Lineham's lower log camp, S. Fork Sheep Creek), and the rest from ca. 25 or 20 mi. SW Calgary ("near the spruce woods"), July 5 to 20 (no years given). The holotype and allotype are in the United States National Museum, and six paratypes are in the Canadian National Museum.

FOOD PLANTS

Langer (in litt.) mentions that European texts list *Rumex* and *Polygonum* as larval foodplants for *phlaeas* forms. Yokoyama (1955) lists "daikon" (a type of garden radish) and various grasses as larval foodplants for *Lycaena phlaeas daimio* Seitz in Japan. This was the only reference we found that listed foodplants other than members of Polygonaceae for *phlaeas* subspecies. *Rumex* species are given as foodplants for *L. p. americana* Harris in various U. S. texts (see Davenport & Dethier, 1937; Klots, 1951). The only reference we found to a foodplant of the three subspecies studied was that of M'Lachlan (1878) to *Oxyria*. He suggested that *Oxyria digyna* (L.), then known as *O. reniformis*, probably serves as the foodplant for *feildeni* since no *Rumex* was found "at all the stations" while *Oxyria* was. Wyatt (in litt.) found *feildeni* at Coppermine, N. W. T., always in association with "a very *Rumex*-like plant" with reddish seeds and 6-8 inches high.

The foodplant for "*hypophlaeas*" in the Sierra Nevada Mountains of California is almost certainly *Oxyria digyna*, Mountain Sorrel, although evidence at present is circumstantial. No specimens of "*hypophlaeas*" were found by us more than a quarter mile from *O. digyna*. Both of us independently have seen females slowly flutter over *digyna* plants (one was seen doing so at 12:35 P.S.T., July 28, 1966, Mt. Dana, Mono County) and repeatedly alight on the flower heads without feeding. One female on August 4, 1964, Mt. Dana, walked extensively on a *digyna* plant. No such activity by females was seen directed toward other plants. However, no oviposition or abdominal

probing by these females was seen. At the Mt. Dana locality, no *Rumex* was found growing on the slopes where "*hypophylaeas*" flies. Flying, feeding, and sunning of both sexes were confined to the extensive *digyna* colony there. One of us (JCM) found "*hypophylaeas*" in four or five localities where *digyna* was found.

The distribution of *O. digyna* is characterized by Mooney & Billings (1961) as "arctic-alpine circumpolar, with disjunct locations far to the south in the mountains of Europe, Asia, and North America." The North American range of *digyna*, as figured by them, encompasses the known localities for *arethusa*, *feildeni*, and "*hypophylaeas*" (see fig. 3).

Mooney & Billings (1961) found that *O. digyna* in North America can be classed into two primary morphological groups. Based on stamen number, inflorescence branch number, and presence or absence of rhizomes, one group includes "all the populations from southern Alberta southward in an area largely to the south of maximum Pleistocene continental glaciation. The other group includes all of the northern populations (p. 27)." Presuming that *digyna* is the foodplant for the subspecies considered here, *arethusa* and "*hypophylaeas*" would correspond to the southern *digyna* populations, and *feildeni* would correspond to the northern populations. (We do not rule out the possibility that these populations may have other larval foodplants.)

Klots (1951) lists *Rumex acetosella* L. and "perhaps" *R. acetosa* L. and *R. crispus* L. as larval foodplants for *L. p. americana*. These are all introduced weeds from Europe and Asia (Fernald, 1950; Munz & Keck, 1965). In California, *R. acetosella* is found in cismontane areas, and *R. crispus* is found in low areas (Munz & Keck, 1965). The California "*hypophylaeas*" apparently has not extended its range into the habitats of these two weeds.

HABITAT

One of us (JCM) found adult feeding confined to a small yellow composite at four localities for "*hypophylaeas*." The other (OS) found feeding by both sexes at the Mt. Dana locality occurring on a number of small alpine flowers and a large yellow composite. At all localities we checked, the males often flew rapidly over the steep talus slopes and alighted to sun themselves on rocks; most of the females were collected while feeding on flowers. Both sexes perched on rocks and sunned either toward or away from the sun. One male on July 28, 1966, Mt. Dana, 11:20 P.S.T., lit on an *O. digyna* flower head momentarily.

MacNeill (in litt.) says that "*hypophylaeas*" at Mono Pass, Mono Co., California, is partial to the rocky "nunatak"-like plateaus

of gentle relief and the slopes of these near their base in the small canyons and chutes.

One of us (JCM) twice took "*hypophlaeas*" in conjunction with *Lycaena cupreus* (Edwards) and *L. editha* (Mead). Neither of these species flew directly with "*hypophlaeas*" at the Mt. Dana locality (see fig. 6), although both did fly some 500 feet lower in elevation to the west.

Legge (in litt.) says that *arethusa* at Plateau Mt. in Alberta is found in small grassy meadows, while *L. cupreus snowi* (Edwards, will fly over the talus as near as few hundred feet away.

Scott (in litt.) says that *phlaeas* ssp. at Halfmoon Park, Sweet Grass Co., Montana, flew in the Hudsonian zone; these were taken on a rocky jeep road in the trees below a barren rockslide.

ADULT MORPHOLOGY

The British Museum of Natural History contains one male and three females of a *phlaeas* form labelled "California, Felder Colln." These specimens are very similar to Eastern U. S. *americana* except that the upper forewing spots are elongated inward. An aberration of *americana* named *fasciata* (Strecker, 1878) has these elongated spots (see no. 18, fig. 1). Brower & Brower (1954) obtained *fasciata* individuals under uncontrolled rearing conditions and speculated that the condition is genetically determined. Lees (1963), however, produced this form environmentally. He reared ten *L. phlaeas* from Ilkley, England, at 35° C., a temperature much higher than the insect normally encounters. His description and illustration of the female adults correspond closely to the B.M.N.H. California specimens. No such ruddy coloration or spot formation was noted in 104 "*hypophlaeas*" specimens we have examined from the Sierra Nevada Mountains. Perhaps the four Felder specimens came from a warm habitat or were reared under heated conditions.

Figures 1 and 2 illustrate geographical variation in North American *L. phlaeas*. Certainly long series from many places coupled with experiments to determine how much of the variation may be due to environmental influences will be necessary to establish the status of the names *arethusa*, *feildeni*, and *hypophlaeas*. Figure 4 illustrates the variation in one population of "*hypophlaeas*" collected on three different years .



Fig. 6. Rocky slope habitat of "*hypophlaeas*" at N. slope Mt. Dana, Mono Co., California.

ACKNOWLEDGMENTS

We wish to thank the following people for loaning specimens or for contributing records and information to this study: W. D. Billings, F. H. Chermock, J. D. Eff, J. G. Franclemont of Cornell University (CU), T. N. Freeman of the Canadian National Museum (CNM), J. S. Garth, J. A. Justice, T. W. Langer, J. A. Legge, C. D. MacNeill, L. M. Martin of the Los Angeles County Museum (LACM), C. W. Nelson, F. H. Rindge of the American Museum of Natural History (AMNH), J. A. Scott, G. E. Tite of the British Museum of Natural History (BMNH), T. P. Webster, and C. W. Wyatt. Our thanks also go to P. McHenry for supplying some original descriptions, to R. Brock for translation of a passage in Japanese and to M. Evans for the color prints.

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LIFE HISTORIES OF THREE WESTERN SPECIES OF *POLITES*

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THE EARLY STAGES OF three western species of *Polites*, one of which is very common, have apparently not been studied thoroughly. This paper discusses the life histories of *P. sabuleti* (Bdv.), *P. sonora* (Scud.) and *P. mardon* (Edw.).

METHODS OF REARING

It was found that females would oviposit readily in the small glass containers that season salt, dill salt and various other seasonings come in. These are about 1½ x 4 inches in size and they have perforated plastic caps. The holes in the tops prevent too much moisture from accumulating but do not allow the skippers to escape. A small piece of absorbent material saturated with a sugar solution can be placed inside, held at the top of the bottle by the cap, on which the females will feed. Oviposition occurs either on grass placed in the bottle or on the sides of the bottle. Females will live for three of four days under these conditions and may deposit as many as 25 eggs during this time.

Newly hatched larvae were put into salve boxes with pieces of grass which was renewed daily. A damp piece of paper towel in the bottom kept the grass from drying out rapidly. Larvae of these skippers develop slowly and when they are fairly large, they may be transferred to the same type of bottles used for oviposition, where they will conclude their development and pupate. They usually spin a loose cocoon among the pieces of grass in which pupation takes place.

POLITES SABULETI

This species occurs from Washington to Arizona and east to Colorado. In the Yakima Valley, Washington, there are two broods, one flying in May and June and the other in August and September. *Sabuleti* seems almost to have become domesticated

in that it has adopted the lawns in cities and towns as its principal habitat. In the Yakima Valley, at least, it is seldom seen elsewhere. In this habitat the larvae feed on lawn grass, which is usually a mixture of Kentucky bluegrass and other species, and the adults feed on the blossoms of wild morning glory, dandelion and other garden flowers. Comstock (1927) states that the larvae "feed on *Carex filifolia* and *Trifolium monanthum*." The former is a sedge occurring from British Columbia and Saskatchewan to California and Texas, and the latter is a clover occurring only in the Sierra Nevada Mountains of California and Nevada. I tried feeding larvae of *sabuleti* on the sedge and also on various clovers, but they would not eat any of these plants. Since the normal food of *Polites* is grass, it is reasonable to expect this to be true of *sabuleti*.

Duration of the egg stage was 7 days at room temperature. The larval period lasted 35 to 50 days and the pupal period 10 to 13 days. Eggs deposited about May 10 produced adults July 19 to 26, and eggs deposited May 21 produced adults July 21 to 26. Hibernation of the second brood is in the pupal stage.

DESCRIPTION

Polites sabuleti

EGG. — Basal diameter 1.0 mm, height 0.8 mm. Color light bluish green, darker at micropyle. Dome-shaped, base flattened. Finely reticulate.

LARVA. — FIRST INSTAR. — Head width 0.5 mm, shiny black. Body length 2.0 mm, light cream; cervical shield narrow, dark brown, a few setae.

SECOND INSTAR. — Head width 0.8 mm, shiny black with numerous fine setae. Body length 4 mm, greenish with many small brown dots, each bearing a seta.

THIRD INSTAR. — Head width 1.1 mm, color and setae as before. Body length 7.0 mm increasing to almost 10 mm, grayish green with many brown dots and brown setae of various lengths; dark median line and a distinct dorso-lateral line; cervical shield black.

FOURTH INSTAR. — Head width 1.6 mm, color as before but with two whitish streaks anteriorly and a shorter one laterally. Body length 10.0 mm growing to 15.0 mm, grayish brown with dark median line, lighter ventrally; suranal plate becoming pronounced, light colored; thoracic legs black; spiracles on first segment large, black, others smaller, brown.

FIFTH INSTAR. — Head width 2.5 mm, color as before, punctate and with fine setae. Body length 18.0 to 22.0 mm, ground color light gray with numerous small brownish patches giving it a griseous appearance, lighter ventrally; median line brown but not sharply defined; numerous fine setae; cervical shield black; suranal shield white with a dorsal and two lateral black streaks; spiracles dark shiny brown; thoracic legs black; prolegs gray.

PUPA. — Length 16 mm, width at thorax 4 mm; color greenish with some brown on head, tips of legs and last two abdominal segments; numerous fine setae dorsally and a few laterally and ventrally on the abdomen. Cremaster short, not emarginate, with a single cluster of hooks.

POLITES SONORA

This is a common species occurring from British Columbia (Llewellyn Jones, 1951) to California and east to Montana, Wyoming and Colorado. In the Northwest, I have taken it on the prairies south of Olympia, Washington, and in Oregon along the upper Rogue River in Douglas County and at Camp Sherman in Jefferson County. The larval foodplant has not been determined, but *Festuca idahoensis* Elmer¹ is very common on the Washington prairies, it occurs throughout the range of *sonora*, and it is probably at least one of the foodplants. The larvae were easily reared on lawn grass and they also fed on *F. idahoensis*. The adults feed on various flowers growing in the habitat.

Duration of the egg stage was 8 days at room temperature. Larvae hatching at the end of June were carried through until the end of July, when they had reached the third instar. No larvae were reared beyond this stage.

¹DDetermined by Professor Marion Ownbey, Washington State University, Pullman.

DESCRIPTION

Polites sonora

EGG. — Basal diameter 1.0 mm, height 0.7 mm. Color very light green. Spherical with small flattened base, not flanged. Finely reticulate.

LARVA. — FIRST INSTAR. — Head width 0.6 mm, shiny black. Body length 1.75 mm, creamy white, a few setae on last two segments; cervical shield black.

SECOND INSTAR. — Head width 0.75 mm, black. Body length 3-5 mm, greenish, covered with numerous minute brown dots; cervical shield black.

THIRD INSTAR. — Head width 1.0 mm, solid black, punctate. Body length 5 mm, grayish green with many fine black setae and a few longer ones on posterior segment.

POLITES MARDON

Polites mardon was described in 1881 by W. H. Edwards (Edwards, 1881) from three males and three females "taken at Mt. Hood" in Oregon by H. K. Morrison. It has been scarce, but has since been taken near Tenino, Thurston County, Washington, by D. L. Bauer, at Grand Mound, also in Thurston County, by J. F. Gates Clarke, on the south slope of Mt. Adams, Yakima County, Washington, at about 6500 feet elevation by Stanley G. Jewett, and on the open grassy slopes of Signal Peak, Yakima County, Washington, at 4800 to 5000 feet by the writer. It has also been reported from Seattle. A search of the area about Tenino and Grand Mound on June 6 and 20, 1966, by the writer did not turn up any *mardon*, although *sonora* was found there at that time. It is possible that *mardon* flies earlier. The Mount Adams and Signal Peak locations are about 55 miles north and 70 miles northeast of the type locality, respectively.

Festuca ovina L.² is abundant on Signal Peak, as is *Bromus carinatus* Hook. & Arn.,² and one or both of these grasses may be the native foodplant. The larvae feed readily on lawn grass, however. The adults feed on the blossoms of dandelion and wallflower (*Erysimum capitatum* (Dougl.)). Males are often seen resting on rocks or bare patches of soil.

Duration of the egg stage was 6-7 days at room temperature. The larval period yasted about three months. Hibernation is in the pupal stage.

DESCRIPTION

Polites mardon

EGG. — Basal diameter 1.0 mm, height 0.8 mm. Color cream becoming yellow-orange. Spherical, base flattened, not flanged. Very finely reticulate.

LARVA. — FIRST INSTAR. — Head width 0.5 mm, light brown. Body length 3.0 mm, very light brown with transverse rows of darker brown dots and a few setae; cervical shield black.

SECOND INSTAR. — Head width 0.75 mm, color as before. Body length 5.0 mm, color as before.

THIRD INSTAR. — Head width 1.0 mm, dark brown with a darker narrow dorsal stripe. Body length 6.5 mm, color as before.

FOURTH INSTAR. — Head width 1.5 mm, color as before. Body length 8.0 mm, color as in third instar but with a darker dorsal stripe.

²Determined by Professor Marion Ownbey.

FIFTH INSTAR. — Head width 2.0 mm, black with two lighter dorsal stripes, surface covered with small pits. Body length 16.0 mm, tapering anteriorly; color light gray, sprinkled with numerous dark brown dots of irregular shape and varying size; a black median stripe; cervical shield black, suranal shield with dark margin and three dark spots just behind anterior edge; ventral surface same color as dorsal; spiracles and thoracic legs black.

PUPA. — Length 15.0 mm, width at thorax 4.0 mm. Smooth without protuberances. Color ashy gray with some light brown areas on abdominal segments and "shoulders" of wings; dorsum of thorax darker gray, darker spots of various sizes scattered over thorax, abdomen and wings; eyes rich brown, darker posteriorly; many fine, light brown setae on abdomen and several tufts of them about the eyes and elsewhere on the head. Cremaster acute, laterally emarginate, hooks many, in dense cluster, scorpionoid.

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KNOW YOUR AUTHOR

BRYANT MATHER

Born: Baltimore, Maryland, December 27, 1916.

Johns Hopkins University, A. A., 1936

Johns Hopkins University, graduate work

American University

Positions: Curator (Mineralogy), Field Museum of Natural History (1939-1941). Geologist, Corps of Engineers, U. S. Army, West Point and Mt. Vernon, New York. Research Engineer, Corps of Engineers, Jackson, Mississippi, 1946 to present.

Began , jointly with K. Mather in 1946, a survey of lepidoptera of Mississippi, now extended to include neuroptera and trichoptera. Author of papers on lepidoptera in Jour. Miss. Acad. Sci., Maryland Naturalist, Lepid., Jour. Lep. Soc., and co-author (with K. Mather) of "Butterflies of Mississippi," Tulane Stud. Zool., 6:63-109, 1958.

Interested in the occurrences of lepidoptera, neuroptera, and trichoptera in Mississippi. Offers specimens of lepidoptera, neuroptera, and trichoptera, mostly from Mississippi for determination and study.

Member: Am. Inst. Biol. Sciences, Lep. Foundation, Lep. Soc., Ent Soc Canada, Nat. Hist. Soc. Md., Miss. Acad. Sci., Am. Assn. Adv. Sci. (Fellow), Phi Beta Kappa, American Concrete Institute (President, 1963-64).

Reference: Euphyes dukesi, J. Res. Lepid., 2:161-169, 1963.

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OVERCOMING DIFFICULTIES WITH
THE PUPAE OF *EUPROSERPINUS*
PHAETON MOJAVE (SPHINGIDAE)

NOEL McFARLAND

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ON APRIL 18, 1957, I collected over 30 last instar larvae of *Euproserpinus phaëton mojave* Comst., in a small area near Llano, Los Angeles County, California (at 3200 feet elevation on the western Mojave Desert). Around 10:00 A.M., many of the larvae were feeding on certain species of the abundant small annuals that cover the desert after a winter of ample rainfall. Those observed feeding were eating *Coreopsis bigelovii* (Gray) Hall, and two small, annual *Oenothera* spp. Those not feeding were either crawling over the ground to other plants, or quietly sunning themselves on the warm sand.

Although the larvae are marked with black, pink, and white on a soft green ground-color, they do not stand out conspicuously when in the natural habitat, because during the short time they are present as nearly fullgrown larvae, the sand around them is covered (to a varying degree) with brightly-colored petals, both fresh and dry, which have fallen from the many ephemeral spring flowers. These fallen petals (which are mostly pink, white, yellow, or blue) blow over the sand and collect in small depressions, or underneath plants where the larvae are feeding and resting.

These collected larvae were transported to the Santa Monica Mountains near the coast (where I was living), and they were offered the leaves of the large, biennial *Oenothera hookeri* T. & G., which was accepted casually. Other possible foodplant substitutes were not available, but as most of the larvae were about to pupate, this was not a problem. In order to approximate conditions in the natural habitat, the larvae were placed outdoors, in a screen-covered 15-gallon aquarium, in the bottom of which



Fig. 1. *Euproserpinus mojave* (adult, 3 views of Larvae).

was about 3 inches of sand from the habitat. They showed an interest in active feeding *only* after they had had a sufficient sunning each morning. Soon, they burrowed into the sand to make underground cells, in which they all pupated successfully. The pupae were dug up about two weeks later, and were stored in a suitable container, indoors, for the diapause period (*i.e.* — from May, 1957 until the following March). During the diapause period, the pupae were kept nearly dry, but for an occasional sprinkling, and they were overwintered outdoors in Albuquerque, New Mexico, where I spent the school year of 1957-1958. (Winter temperatures in that locality approximate those on the high Mojave Desert). They remained in excellent condition the whole time, responding with abdominal movement when handled. However, when it came time for them to emerge (in March, 1958), problems developed. By late March, maculation on the forewings of the developing moths was easily visible through the pupal shells, so it was assumed that warmer temperatures, plus dampened soil, would bring about emergence in short order. The pupae were in a non-toxic, clear plastic box, on top of about one inch of the original sand from the habitat. The sand was then kept lightly damp. In most of the pupae, the moths were developed to the full extent, appearing ready to emerge at any moment, and at last they reached the final stage (just prior to emergence) where there is expansion between the abdominal segments of the pupa. But nothing happened thereafter! The pupae would not emerge after reaching that point of readiness; if they were opened by hand, the moths scrambled out in apparent good health, but the wings always failed to expand. If the pupae were left alone, the moths finally died within them, never emerging. When all but one of the pupae had been lost in one way or the other, something different was tried with the one remaining healthy pupa, which was ready to emerge in mid April. On April 18, 1958, the plastic box containing this pupa (lying upon damp sand), was placed in the sun at about noon. The box "steamed" inside. Shortly the moth emerged of its own accord! Then another detail was observed: The newly-hatched moth did *not* seek a place where it could climb up, in order to let its wings hang down as they expanded and dried (which is the normal procedure with most freshly-emerged moths). Instead, the moth continued to sit on the damp sand, in the sun, and its wings rapidly "mushroomed" straight *upward* as they expanded. Then they were held erect, over the thorax. Full ex-

pansion of the wings took less than one minute, once started. When the box was taken out of the sun for a moment, the moth showed immediate distress and began running about; its limp, newly-expanded wings fell down and dragged on the ground as the moth ran. Upon being replaced in the sun, the moth stopped running and the wings again went straight up, and were held that way (together) until dry. A few minutes later, the fully-developed moth was flying around inside the box. It was subsequently spread for the collection. (See the photograph of this reared specimen, and three unhatched pupae).

This account illustrates one of the difficulties sometimes encountered by those who would rear Lepidoptera — the problem of breaking pupal diapause, and/or causing emergence of the imago; this problem is very commonly encountered when attempting to rear species from arid regions. Although the treatment described above was successful with the diurnal, sun-loving *Euproserpinus*, that procedure would not necessarily succeed in causing emergence in very many other cases, except, possibly, with other diurnal desert moths. If such a technique is tried, the pupae should not be sun-warmed until the day they appear completely ready to emerge; then, the sun must not be too hot, the soil should be damp, and conditions in the container holding the pupae should be watched closely, to avoid over-heating.

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SPEYERIA CYBELE IN MISSISSIPPI ¹ ²

(ARGYNNINAE: ARGYNNIS)

BRYANT MATHER

Box 2131, Jackson, Miss. 39205

MATHER AND MATHER (1958) listed *Speyeria cybele cybele* (Fabricius) among the butterflies that were not then known to have been found in but were of probable occurrence in Mississippi. They noted that Lambremont (1954) had reported one male taken at Lafayette, La. on 2 October 1931, in the collection at Southwestern Louisiana Institute; that H. A. Freeman (1951) had reported it as usually rather scarce in Arkansas; and that Roeber had taken it in southwestern Tennessee. They noted that dos Passos and Grey (1947) had listed it for Tennessee, Illinois, Arkansas, and Oklahoma; but not for Mississippi or Louisiana.

In October 1960 in a butterfly collection displayed at the Mississippi State Fair by Miss Lynn Schabilion of Rolling Fork, Miss. there was a specimen of *S. cybele*. Upon investigation it was determined that this specimen had been collected in Arkansas. Through the courtesy of Dr. Gordon Gunter, Director, Gulf Coast Research Laboratory, Ocean Springs, Mississippi, we were put in touch with Dr. E. Avery Richmond of Moorestown, New Jersey, who was compiling data on the flora and fauna of Horn Island. This work has now been published (Richmond, 1962), and includes *Speyeria cybele cybele* (Fabricius). Dr. Richmond has informed me (in litt.) that his records indicate that this specimen was taken on 23 September 1944; they do not indicate the determiner of the specimen or the disposition of the specimen. Most of the determinations were made at the U. S. National Museum. In January 1962 a search was made of the collections

¹ In this note the name "*Speyeria cybele cybele* (Fabricius)" is used to conform with previous usage in current relevant literature (Mather and Mather 1958; Klots, 1951; Ehrlich and Ehrlich, 1961; and dos Passos, 1964). For a discussion of an alternative usage, see Hovanitz (1962). The butterfly with which this note is concerned has been given the common name "Great Spangled Fritillary."

² Editorial Note: In the *Journal of Research on the Lepidoptera*, name usage is the personal prerogative of the author, and is not an editorial matter. The editor prefers that authors use names of general significance, rather than of local preference. However, as is the practice in all entomological journals, when the name of a smaller taxonomic group is used in a title, a larger group of which the smaller is part, is shown in parenthesis for the orientation of the reader. This should aid bibliographers looking for various Argynnis.

there and it was established that no specimen of *S. cybele* from Mississippi could be found. It was thus concluded that while this constituted a probable occurrence it could not be regarded as a confirmed record.

On 10 June 1963 at Oxford, Lafayette Co., Miss., Mr. John L. Daniel took by hand, in the afternoon, a male *S. cybele* which is now before me. The specimen has a forewing of 40 mm. It was taken while feeding on flowers of cultivated marigolds.

On the basis of this record *Speyeria cybele cybele* (Fabricius) is added to the list of butterflies known to have been taken in the state of Mississippi. The range of this species, which has been given as "... to North Carolina and Georgia (mountains), Tennessee, Arkansas, and Oklahoma" (Klots, 1951) and as "... to North Carolina, Georgia, Arkansas, Oklahoma ..." (Ehrlich and Ehrlich, 1961), can now be given "... to Georgia, Tennessee, Mississippi, Louisiana, Oklahoma ..."

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Euphyes dukesi — Additional Record

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Following publication of the review of knowledge of this species, (Mather, 1963), Mr. H. A. Freeman wrote (in litt.) that he had recently found among his specimens a ♀ *E. dukesi* that had been collected by him at Hope Hill Farm, Faulkner Co., Arkansas on 29 June 1947. This locality, somewhat north of Little Rock in central Arkansas, represents a westward extension of the known range and adds an eighth state to the list of those from which it is now known.

REFERENCE

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THE LITTLE KNOWN MOTH *EUXOA SCULPTILIS* (HARVEY) IN ARIZONA,

WITH DESCRIPTIONS, ILLUSTRATIONS, AND NOTES ON *EUXOA*
VIOLARIS (GROTE AND ROBINSON) (NOCTUIDAE-AGROTIINAE)

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EUXOA SCULPTILIS (HARVEY) WAS DESCRIBED from specimens collected in Texas, and until recently has been poorly known in collections. This species is in the adult stage during the autumn months, and because of its occurrence during this late time of year, most collectors have not taken species. *E. sculptilis* has been collected from the first part of October into early December, and without the aid of a collector-in-residence, the large series at hand would probably not have come before the author. Nothing is yet known concerning the immature stages of this species.

Since the original description of *sculptilis* in 1874, the species has been shifted from *Agrotis* to *Ammaconia* to *Richia* to *Carneades* to *Paragrotis* and finally to *Euxoa* in 1903 by Hampson, where it is presently placed by most authors. Strangely enough, *Euxoa violaris* (Grote and Robinson), the most closely related species to *sculptilis*, was not even placed in the genus *Euxoa* until McDunnough (1928) in his generic revision of the North American agrotid moths, placed it next to *sculptilis*. *E. violaris*, as in the case with *sculptilis* is poorly represented, or entirely lacking in most collections.

"*Carneades*" *xyliniformis* Smith was described in 1890, and Smith stated "This species is unique in appearance and has a striking habitual resemblance to *Litholomia napae*." He further stated "The species is unique wherever placed, and is readily recognizable." "*C.*" *xyliniformis* is conspecific with *E. sculptilis*, and therefore was placed into synonymy by Smith (1893). *E. sculptilis* is quite distinctive (as can be seen in figures 1 and 2)



Fig. 1. *Euxoa sculptilis* (Harvey), male. Madera Canyon, Santa Rita Mountains, Santa Cruz County, Arizona, ele. 4880', 17 November 1966 (D. N. Harrington).

Fig. 2. *E. sculptilis*, female. Same data as preceding.

and does remind one of *Litholomia napae* in general appearance. Hampson's colored illustration of *sculptilis* is quite good, and will readily aid in identification of this species; whereas,

the colored illustration by Draudt (in Seitz, 1923) is altogether off color and the shape of the forewing is not correct either.

EUXOA SCULPTILIS (Harvey)

Agrotis sculptilis Harvey, 1874. *Bull. Buffalo Soc. Nat. Sci.* 2:271.

MALE: Ground color of primaries transversely bicolor, basal one-half silvery grey, terminal one-half blackish grey; secondaries dirty whitish. Head with vertex clothed in elongate, blackish flattened hairs, white tipped, hairs porrect so as to form eyelash-like tufts over base of antennae; between antennae a transverse black bar is present; frons also with eyelash-like divided tufts dorsally, composed of dark brown white-tipped flattened hairs and white scales; beneath eyelash-like tufts, and between compound eyes a coal black broad transverse band is present, composed of simple and flattened elongate hairs; beneath this band, a tuft of brownish, white-tipped elongate flattened hairs, one each exterolateral of frons; central portion of frons of brown short hairs; frons roughened, centrally with ovate protrusion, pointed end directed dorsally, palpi with apparent basal segment exterolaterally black, ventrally clothed in brownish; second segment exterolaterally composed of brownish scales, ventrally clothed in elongate black, greyish brown and whitish hairs; third segment short, less than one-half length of second segment, clothed in greyish and blackish scales; antennae with scape, pedicle clothed in brown, reddish-brown and dark brown elongate hairs, elongate, dentate scales; flagellomeres bi-serrate, bipectinate, pectinations and serrations becoming reduced to ciliations and filamentous apically. Thorax with collar composed of reddish brown elongate hairs and elongate dentate scales, with two bilobed transverse bands, one basally, another medially; scales and hairs between bands white-tipped; slight anterior tuft composed of bicolor, basally brown, apically dark brown, white-tipped elongate hairs; disc composed as is anterior tuft; tegulae conspicuously of black elongate dentate scales and hairs, with inner margin possessing a band of brownish, white-tipped, elongate dentate scales; posterior tuft basally brown, preapically dark brown, apically white-tipped; posteriorly with elongate simple, silken hairs; at base of forewing, and beneath it, a bunch of deeply cleft elongate scales forms a yellowish-red cluster; primaries dorsally transversely bicolor; basal one-half of surface heavily overlain with white scales, therefore appearing grey; basal half line geminate, black, centrally grey



Fig. 3. *Euxoa violaris* (Grote and Robinson), male. Lakehurst, New Jersey, 21 September 1910 (F. Lemmer).

Fig. 4. *E. violaris*, female. Long Island, New York, 29 September 1900.

filled, very distinct; basal and transverse anterior area contiguous on inner margin; transverse anterior area grey, centrally with white dot; transverse anterior line black, very distinct, geminate,

centrally filled with grey, from where transverse anterior line intersects 2dA vein to where it reaches inner margin, it bows apically, therefore appearing like a geminate subclaviform; median area to median shade grey; claviform distinct, neatly outlined in black; orbicular large, more triangular than round, neatly outlined in black, thence white, centrally filled with grey; median shade black, contrasting markedly with grey portion of median area; remainder of median area dark brown, costally with light brown scales; transverse posterior line represented on costa just above reniform, appearing as geminate black dash, thence undulating out around reniform and very faintly on to inner margin; subterminal area dark, but with more grey than adjoining median area; subterminal line represented costally as dark wedge, thence hardly discernable; terminal line represented as black lunules between veins; fringes basally light brown, remainder smokey; ventral surface bordered in grey, medially brownish; transverse posterior line represented as black costally, thence a very faint line on to inner margin; secondaries dorsally whitish; inner margin with brown scales and hairs; veins outlined in brown; terminal line dark brown; fringes tricolor, basally light brown, medially brown, apically white-tipped; ventral surface whitish, costal margin irrorated with black so as to form faint dark band; exterior line thin, black; fringes whitish, becoming darker toward apex; ventrally, thorax clothed in brownish, white-tipped simple hairs; legs with profemora dorsally black, ventrally composed of elongate white-tipped, brown simple hairs; protibiae heavily spined; tarsi dark brown, a suggestion of a lighter apical annulus on each tarsomere; ungues weakly bifid. Abdomen dorsally clothed in brown and white simple elongate hairs and elongate dentate scales; ventrally clothed in elongate, brown, white scales. Greatest expanse of forewing 16mm to 19mm. Genitalia as in figures 6 and 7.

FEMALE: For all practical purposes, as in male, except antennae simple, ciliate, thorax lacking basal bilobed black band of collar; primaries slightly darker; secondaries dorsally fuscous. Greatest expanse of forewing as in male, may average very slightly larger. Genitalia as in figure 5.

Specimens examined

One male, Madera Canyon, Santa Rita Mountains, Santa Cruz County, Arizona, ele. 5880', 19 October 1959 (J. G. Franclemont), Bauer-Buckett slide No. NY63L11-15; 1 female, same locality and collector as preceeding 7 October 1959, Bauer-Buckett slide

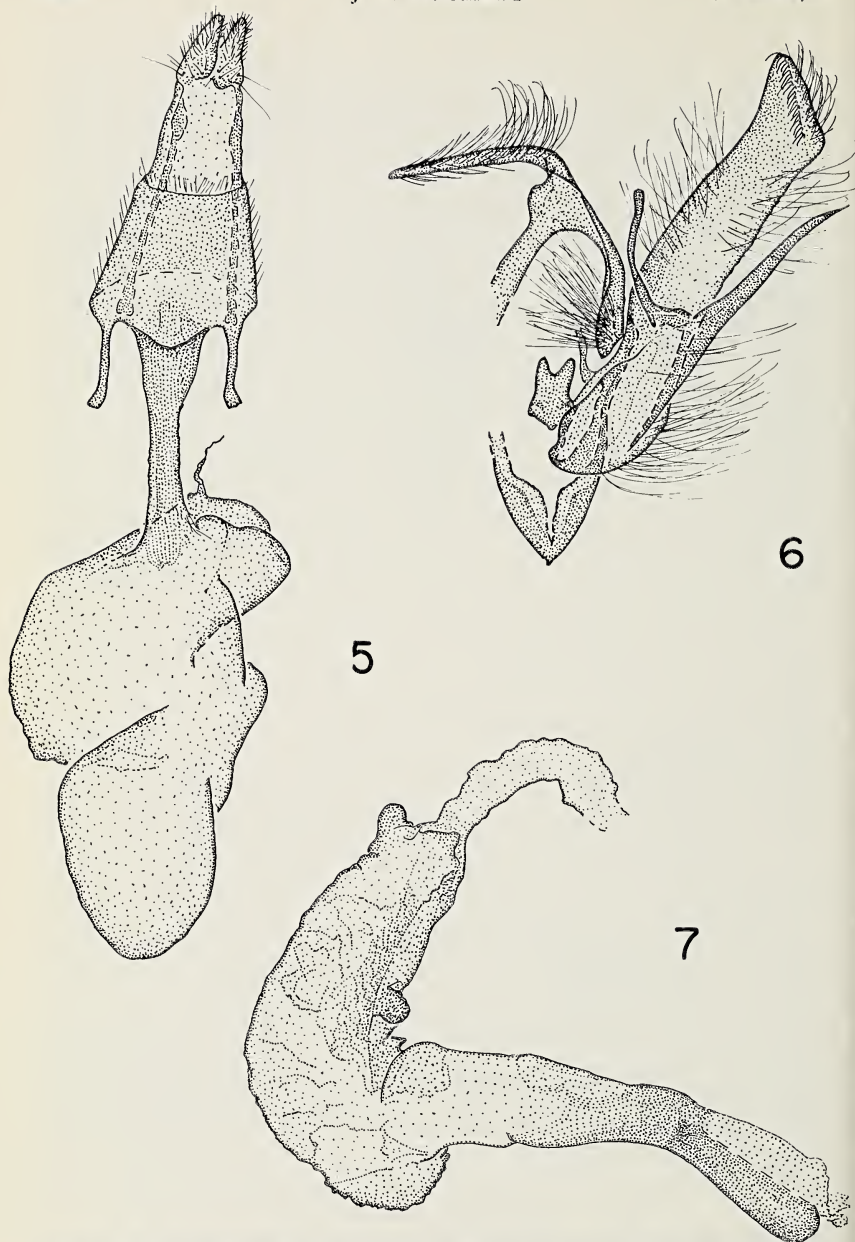


Fig. 5. *E. sculptilis*, female genitalia. Madera Canyon, Santa Rita Mountains, Santa Cruz County, Arizona, 7 October 1959, ele. 5800' (J. G. Franclemont), Bauer-Buckett slide No. NY63L11-16.

Fig. 6. *E. sculptilis*, male genitalia minus aedeagus. Locality and collector same as preceding, 19 October 1959, Bauer-Buckett slide No. NY63L11-15.

Fig. 7. *E. sculptilis*, aedeagus of male genitalia. Data same as for fig. 4.

No. NY63L11-16; remainder of specimens all Madera Canyon unless otherwise stated; 2 males, 2 females, 8 October 1963 (V. L. Vesterby); 1 male, 5 November 1965 (D. N. Harrington), Bauer-Buckett slide No. 66C31-1; 1 female, 5 November 1965 (D. N. H.), Bauer-Buckett slide No. 66C31-2; 8 males, 9 females, 2 November 1966 (D. N. H.); 1 male, 7 October 1965 (D. N. H.); 20 males, 25 females, 2-5 November 1965 (D. N. H.); 15 males, 8 females, 21-28 October 1965 (D. N. H.); 4 males, 14 October 1965 (D. N. H.); 3 males, 6 December 1965 (D. N. H.); 16 males, 21 females, 27 November 1965 (D. N. H.); 15 males, 27 females, 14 November 1965 (D. N. H.); 1 female, Kerrville, Texas, with label "det. & pres. by Wm. Barnes."

Over 200 specimens of *sculptilis* were examined from the southwestern United States, the majority of these being from Madera Canyon, Santa Rita Mountains, Santa Cruz County, Arizona, elevation 4880'. Specimens were also collected at 5800' elevation in Madera Canyon. The genitalic slides were prepared while the author was studying under Dr. John G. Franclemont in Ithica, New York, in 1963. Merthiolate instead of ligin pink was used as the stain. Thanks are due Dr. Franclemont for his encouragement and instruction during that most fruitful experience.

At this time I would like to express my appreciation to Master Danny Harrington of Madera Canyon, Arizona for his splendid efforts in collecting moths during the past few years. Without his effort, this presentation would not have been possible.

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DISCOVERY OF
A LARVAL HOSTPLANT FOR
ANNAPHILA LITHOSINA
WITH NOTES ON THE SPECIES (NOCTUIDAE: AMPHIPYRINAE)
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University of California
Davis, California

ON MAY 13, 1967, it was the author's pleasure of discovering larvae and eggs on *Mimulus guttatus* DC. which were thought to be deposited by specimens of *Annaphila lithosina* Henry Edwards. By observation of the *Mimulus* through late morning and early afternoon, oviposition by *lithosina* was observed. This phenomenon was studied quite closely, and occurred between 1:00 P.M. and 1:30 P.M. (Pacific Daylight Saving Time).

The female would hover over small clumps of *Mimulus* for a few seconds, alight on new growth and walk over the area, apparently examining the new shoots for an oviposition sight, and perhaps also in some way attempting to detect the presence of previously deposited eggs by members of the same species. The value of female *lithosina* being able to detect the presence of eggs of her own species would be of paramount importance in exhibiting awareness of food supply versus population density for the immatures to emerge in due time. Whether this "ability" is in reality present in *lithosina* is doubtful, and could only be positively ascertained through timely intricate experimentation; *but*, when females alighted on new growth that already contained what seemed to the observer to be an overadequacy of eggs in relation to the amount of plant material available, they would not oviposit, but would seek another clump of new growth.

When a female located the "desired" clump, she would remain in one position for a few seconds, and while slowly waving her wings up and down, would thrust the abdomen downward between new leaves or sepals, and would either singly deposit

an egg, or would lay up to 10 or 12 in a row. Eggs were also deposited on stems and some of the older growth of the plant. She would then move to another site on the same clump and repeat the same process until a number of eggs had been deposited. On a single stalk of new growth, as many as over 75 eggs were counted.

If gusts of wind would appear in sufficient force to shake the plant vigorously, the female would either return to her hovering above the plant, or would fly away to another clump. If she returned to her hovering position, generally a few inches to nearly a foot above the plant, she would return soon after the gust of wind subsided and continue oviposition. Examination of *Mimulus* flowers yielded one second instar larva, and some damage to petals was evident; however, the majority of flowers examined showed only a few to have been fed on . . . presumably by immature *lithosina*.

The adult *lithosina* abounded in this study area which is located 3 miles east of Auburn, in El Dorado County, California, and a number of specimens were collected with minimal effort. Adults were also collected 15 miles northeast of Auburn, Placer County, again in the close proximity with *Mimulus guttatus*. In previous years the author and associates have collected *lithosina* near the Feather River at Elephant Butte, Plumas County, California and *Mimulus guttatus* was present, but prior to the present time, this species was not a suspect larval host-plant, and therefore was not examined for eggs or larvae.

This year adult *lithosina* were collected in mid morning during which time they were seen to alight on green foliage while exhibiting the typical "wing-waving" pattern so noteworthy of members within the genus. As noon and early to mid afternoon came about, adults were observed feeding on the flowers of *Montia parviflora* (Moq.) Greene, *Nemophila heterophylla* F. and M.; one specimen was taken while in association with *Ranunculus californicus* Benth., but it was not ascertained whether or not the specimen was actually feeding. Another foodplant adult *lithosina* were collected on is *Plagiobothrys nothofulvus* Gray (personal communication with Mr. Terry A. Sears), but the author was unable to locate *lithosina* feeding on this plant species. At no time were any adult specimens of *lithosina* seen feeding on the flowers of *Mimulus guttatus*.

As is usual with the large, succulent form of *M. guttatus*, the specimens concerned were growing at the edge of a stream at

$\pm 2,000'$ elevation where moisture is available well through the flowering season. The surrounding environment is intermixed deciduous and coniferous woodland with occasional meadows to be found. It is possible that *lithosina*, like other members of the genus is host specific on *M. guttatus*, as time may bear out. To my knowledge *M. guttatus* is abundant throughout the known range of *lithosina*.

It is rather interesting to note a peculiar quotation referring to the immature stages of *lithosina* as quoted by Rindge and Smith (1952). It reads as follows: "Larvae feeding in numbers on larvae of wasps. Sacramento, Calif. Harry S. Smith Febr. 16, 1915." It is highly unlikely that this observation (?) is representative of the normal feeding habits of immature *lithosina*, and it is possible that this claim has no foundation in reality. Some lepidopterous larvae will turn cannibalistic when under an ecological stress such as food shortage, but in most instances this habit should not be considered usual. There is no actual proof that the specimen bearing the aforementioned label was one of these wasp consumers, but Rindge and Smith (op. cit.) do state of the specimen "The wings of this specimen, a male, are rudimentary, but a genitalic preparation shows that it is properly referred to this species."

At present, the author is attempting to rear specimens of *lithosina*, and should success occur, detailed descriptions, illustrations and setal maps will be presented in an additional paper. Comparisons are being made between natural populations and laboratory populations in relation to duration from egg to adult. With the large natural population at hand, perhaps the observation of parasites and predators will be made.

A. lithosina is in the species group of the genus comprised of *lithosina*, *miona* Smith, and *casta* Henry Edwards. For a colored photograph of the members of this species groups, see "A reevaluation of *Annaphila casta*" (Buckett, 1966). To my knowledge, no larval hostplant records have been published concerning either *miona* or *casta*, but I believe Mr. Chris Henne (personal communication) has worked these out and will publish the results in the near future.

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- BUCKETT, J. S., 1966 (1965). A reevaluation of *Annaphila casta* (Noc-tuidae). *J. R. Lepidoptera* 4(3):199 - 204.
- RINDGE, F. H., and C. I. SMITH, 1952. A revision of the genus *Annaphila* Grote (Lepidoptera, Phalaenidae). *Bull. American Mus. Natur. Hist.* 98(3)191 - 256.

RECORDS FOR NORTH AMERICAN LYCAENA PHLAEAS
SUBSPECIES (EXCEPT AMERICANA)

CANADA.

ALBERTA. Banff, VII-23-25, "1" (O. Bryant, AMNH). Near Billings lumber mill, Calgary, VII-19-03, "1" (F. H. W. Dod, AMNH). Brobokton Creek, halfway between Lake Louise and Jasper, VII-8, 12, 13, 16-07 (Mrs. Nicholl, BMNH and CNM). Near the spruce woods, 20 or 25 mi. SW Calgary, VII-5 to 20-?, 4 ♂ 8 ♀ (F. H. W. Dod, in Dod, 1907, 6 arethusa paratypes in CNM, ♂ and ♀ "types" in USNM). Crow's Nest Pass, S. Alberta (G. Geddes, in Dod, 1907). Fallentimber Creek, 51° 45' N., 114° 39' W., 5500' (J. Legge). Foothills, Lineham's lower log camp, S. Fork Sheep Creek, ca. 35 mi. SW Calgary, 1 ♂ (F. H. W. Dod, in Dod, 1907). Peyto Lake, Banff Nat. Park, 51° 43' N., 116° 31' W., (fide J. Scott). Plateau Mt., 8200', VIII-2-62, "3" (J. and A. Legge).

BRITISH COLUMBIA. Atlin, 4000', VIII-2-55 (CNM). Moosehorn Lake, 132° 07', 58° 10', 4500' (CNM). Western slopes, Mt. Sidney Williams, N. C. B. Columbia, 54° N., 125° W., ca. 5500', VII-31-53, 1 ♂ (R. J. Gilpin, BNMH). Spray Lake, "2" (in Anonymous, 1962).

NORTH WEST TERRITORIES. Arctic Bay, Baffin Land, VIII-2-42, "1" (AMNH). Baker Lake, VI-30 to VII-7-51 (CNM); "2" (F. H. Chermock). Bathurst Inlet, VIII-1-51 (CNM); "1" (C. Wyatt, in Wyatt, 1957). Bernard Harbour, 68° 45' N., 114° 45' W., VIII-6-15 (CNM). Caribou Valley, head of Clyde Inlet, Baffin Island, VII-31-50, 1 ♂ (V. C. Wynne-Edwards, BMNH). Head of Clyde Inlet, Baffin Island, VII-29-50, 2 ♂ 1 ♀ (V. C. Wynne-Edwards, BMNH); Chesterfield Inlet, VII-?-66, "1" (in Anonymous, 1967); VIII-7-58 (CNM). Coppermine, VIII-2-51 (CNM); late VII-55, "series" (C. Wyatt, in Wyatt, 1957). Cockburn Point, Coronation Coast, 68° 52' N., 115° 0' W., IX-1 to 2-14 (CNM). S. slopes of Dyke Mt., head of Clyde Inlet, Baffin Island, VII-26-50, 1 ♂ (V. C. Wynne-Edwards, BMNH). Eskimo Point, "2" (F. H. Chermock). Falcon Hollow, head of Clyde Inlet, Baffin Island, VII-27-50, 1 ♂ (V. C. Wynne-Edwards, BMNH). Frobisher Bay, Baffin Island, VII-6 to 20-48 (CNM); VIII-?-64, 1 ♂ (J. P. Paton, BMNH). Grinnell Land, W. side of Smith Sound, Lat. 81° 45' (Capt. Feilden; holotype ♂, allotype ♀, and a paratype ♂ in BMNH, in M'Lacklan, 1878, feildeni TL). Hazen Camp, Ellesmere Island, 81° 49' N., 71° 18' W., VII-29 and 30-66; VI-23 to VII-31-61 (Both CNM). Holman, Victoria Island, VII-5-52 (CNM). Lake Harbour, Baffin Island, VII-7-35 (CNM). Mellville Penn., 56° 51' N. [probably 66° 51' N.], 84° 51' W., VII-19-48 (CNM). Pelly Bay, VII-19-52 (CNM). Penny Highland Area, Cumberland Penn., Baffin Island, VIII-5-53, 1 ♂

(A. Watson, BMNH). Repulse Bay, VII-28 to VIII-9-50 (CNM). Southampton Island, VII-5-30, "1" (G. M. Sutton, AMNH); "2" (F. H. Chermock, CM). Wager River, NW Hudson Bay, 65° 26' N., 88° 40' W., "1" (F. H. Chermock).

YUKON. Dawson (CNM). Dry Creek, on Alaska Hwy. near Alaska border, VII 23-48 (CNM). Near Haines Junction, ?-?-66. Yukon Terr., Lat. 64° 31', Long. 138° 30', ?-?-16 (CNM).

GREENLAND. Qânâq, MacCormick Fjord, 77° 41', VIII-26-41, 1 ♀ (C. Vibe, in Wolff, 1964).

UNITED STATES OF AMERICA

ALASKA. Arctic Village, VII-15 and 20-64 (in Anonymous, 1965). Cape Thompson, VII-26- to 29-61 (CNM). Driftwood, 68° 49' N., 161° 09' W., VIII-6-52 (CNM). Highway Pass, McKinley Nat. Park (A. H. Legge, in Legge, 1965). McKinley Nat. Park, VIII-4-31, 1 ♂ (F. Morand, LACM); VII-20 to VIII-1-31, "20" (AMNH). Toklat River, McKinley Nat. Park (A. H. Legge, in Legge, 1965).

CALIFORNIA. Fresno County: near Baboon Lake, VIII-1-60, "sighting" (J. C. Montgomery). Ridge S. of Golden Trout Lake, VIII-4-60, 4 ♂ (J. C. Montgomery). N. side of peak (12,492'), Wahoo Lake, VIII-3-60, 5 ♂ 3 ♀ (J. C. Montgomery). S. side of peak (12,492'), Wahoo Lake, VIII-5-60, 2 ♂ (J. C. Montgomery). Fresno-Inyo County line: Bishop Pass, 12,000', VII-31-60, 1 ♀ (J. C. Montgomery). Mono Pass (C. D. MacNeill). Madera County: W. slope above Emerald Lake, 10,000', 1/4 mi. S. Thousand Island Lake, VIII-14-62, "1" (T. P. Webster). Mono County: W. above Barney Lake, est. 10,200', VIII-4-35, 1 ♂ (L. M. Martin, LACM). Mammoth Mountain, est. 11,000', VII-27-34, 1 ♂ (LACM). N. slope Mt. Dana, NE of Tioga Pass, 11,000-12,000', VIII-8-33, "1" (J. S. Garth); VIII-6-60, 13 ♂ 4 ♀; VIII-7-60, 14 ♂ 6 ♀; VIII-8-60, 4 ♂ 6 ♀; VIII-9-60, 4 ♂ 2 ♀; VIII-13-60, 5 ♂ 2 ♀ (all O. Shields, in Garth and Tilden, 1963); VIII-4-64, 10 ♂ 3 ♀; VII-28-66, 5 ♂ 1 ♀; VIII-6-66, 6 ♂ 4 ♀ (all O. Shields). Tuolumne County: Bert Lake, below Mt. Maclure, est. 11,700', VIII-6-33, 1 ♂ (J. S. Garth, LACM, in Garth, 1935). Cathedral Lake, est. 9000-9500', VII-16-29, "1" (G. E. Bohart, AMNH). Kuna Crest, Yosemite Nat. Park, 11,000', VIII-5-33, 1 ♂ (J. S. Garth, LACM).

MONTANA. Carbon County: Bear Tooth Mtns., VIII-9 to 12-41, "5" (G. H. and J. L. Sperry, AMNH); VII-15-42, "1" (AMNH). Sweet Grass County: Halfmoon Park, Crazy Mtns., ca. 15 to 20 mi. NW Big Timber, VII-3 to 4-66, 2 ♂ 1 ♀ (J. Scott).

WYOMING. County undetermined: Amphitheater Lake, Grand Tetons, 10,000', VIII-?-49, 1 ♀ (V. Nabokov, CU, in Nabokov, 1950). Beartooth Lake, VIII-21-49, 1 ♂ (V. Nabokov, CU). Teton Glacier, Teton Mtns., VII-19-31, "2" (AMNH).

TABLE 1. VARIATION OF H. MELPOMENE AND H. ELEVATUS

Region	<u>elevatus</u>	plate fig.	<u>melpomene</u>	plate fig.
Upper Rio Amazonas	ssp. <u>elevatus</u> Nöid.	A	ssp. <u>aglaope</u> Feld.	F
Rio Huallaga	ssp. <u>pseudocupidineus</u> nov.	—	geographical form <u>flavotenuiata</u> Neust.	—
Eastern and southern Amazonia	ssp. <u>bari</u> (Oberth.)	B	ssp. <u>thelxiope</u> (Hüb.)	G
Bolivia (and north central Amazonia)	ssp. <u>perchlorus</u> J. and K.	C	ssp. <u>penelope</u> Stgr.	—
	ssp. <u>taracuanus</u> Bryk	—	ssp. <u>vicinus</u> (Mén.)	H
Interior of the Guianas	ssp. <u>tunatumari</u> Kaye	D	ssp. <u>meriana</u> Turner = <u>cybele</u> (Cram.)°	I
Guianas	ssp. <u>roraima</u> nov.	E	<u>polymorph eulalia</u> Riff.	—
Other parts of Spanish America	no forms	—	ssp. <u>melpomene</u> (L), <u>timareta</u> (Hew.), <u>amaryllis</u> <u>Feld.</u> , <u>cythera</u> (Hew.), <u>xenoclea</u> (Hew.), <u>corona</u> Niep, <u>nanna</u> Stich., etc., and many polymorphs.	—

° see Turner, J. R. G., 1967, J. Linn. Soc., Lond. (Zool.) 46, 263.

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Volume 5

Number 4

December, 1966

A New Species of <i>Oncocnemis</i> from the Western United States (Noctuidae:Cuculliinae)	John S. Buckett and William R. Bauer	197
Speciation in the <i>Agathymus</i> (Megathymidae)	H. A. Freeman	209
The Eggs and First Instar Larvae of Three California Moths	John Adams Comstock	215
An Additional Food Plant Record for <i>Papilio thoas autocles</i> R. & J.	John Adams Comstock	220
A New Species of <i>Polia</i> Ochseneheimer from California and Notes on <i>Polia discalis</i> (Grote) (Noctuidae:Hadeninae)	John S. Buckett and William R. Bauer	221
Know Your Author — Brian O. C. Gardiner		229
A Gynandromorph of <i>Lycaena gorgon</i>	Paul A. Opler	230
The Distribution and Bionomics of Arctic-Alpine <i>Lycaena phlaeas</i> Subspecies in North America	Oakley Shields and Johnson C. Montgomery	231
Three Western Species of <i>Polites</i>	E. J. Newcomer	243
Know Your Author — Bryant Mather		248
Overcoming Difficulties With The Pupae of <i>Euproserpinus phaeton mojave</i>	Noel McFarland	249
<i>Speyeria cybele</i> In Mississippi. Argynnninae: (Argynnis)	Bryant Mather	253
<i>Euphyes dukesi</i> — Additional Record	Bryant Mather	254
The Little Known Moth <i>Euxoa sculptilis</i> (Harvey) in Arizona, with Descriptions, Illustrations, and Notes on <i>Euxoa violaris</i> (Grote and Robinson) (Noctuidae-Agrotiinae)	J. S. Buckett	255
Discovery of A Larval Hostplant for <i>Annaphila lithosina</i> With Notes on the Species (Noctuidae Amphipyrrinae)	John S. Buckett	262
Appendix to Distribution of <i>Lycaena phlaeas</i>	Oakley Shields and Johnson C. Montgomery	265
Correction to "A Little-recognized Species of <i>Heliconius</i> Butterfly"	John R. G. Turner	267

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

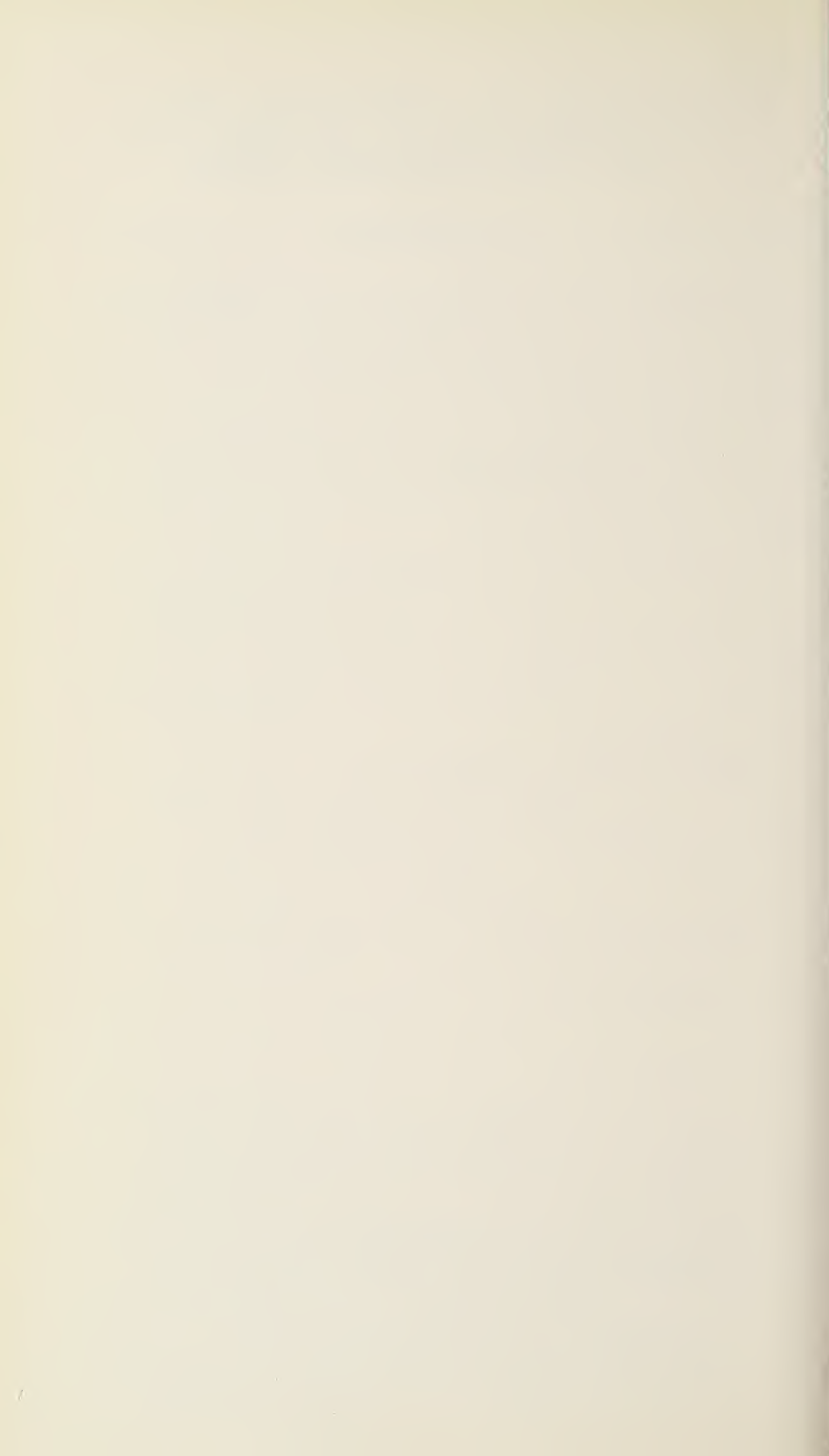
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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

CONTENTS

<i>Volume 6</i>	<i>Number 1</i>	<i>March, 1967</i>
Spring Moths of a Natural Area in Northeastern Kansas	Noel McFarland	1
A New Species of <i>Nepticula</i> on Bur Oak in Ontario	T. N. Freeman	19
Fixation of the Type Locality of <i>Lycaena phlaeas</i> <i>hypophlaeas</i> and a Foodplant Correction	Oakley Shields	22
Description of a New Species of <i>Xylomiges</i> from California	John S. Buckett	23
The Life-Histories of South African <i>Colotis erone</i> , <i>C. ione</i> , <i>C. vesta</i> and <i>Leptosia alcesta</i> (Pieridae)	Gowan C. Clark and C. G. C. Dickson	31
A New Species of <i>Feralia</i>	John S. Buckett	43
Homonymy of the "New Genus" <i>Petaluma</i> and Proposal of the Name <i>Petalumaria</i>	J. S. Buckett and W. R. Bauer	52
Rearing <i>Euleucophaeus rubridorsa</i> and <i>E. lex</i>	Brian O. C. Gardiner	53
The Status of Some Hesperiidæ from Mexico	H. A. Freeman	59
The Generic, Specific and Lower Category Names of the Nearctic Butterflies	Paddy McHenry	65
<i>Volume 6</i>	<i>Number 2</i>	<i>June, 1967</i>

HILLTOPPING

AN ECOLOGICAL STUDY OF
SUMMIT CONGREGATION BEHAVIOR
OF BUTTERFLIES ON A
SOUTHERN CALIFORNIA HILL

OAKLEY SHIELDS

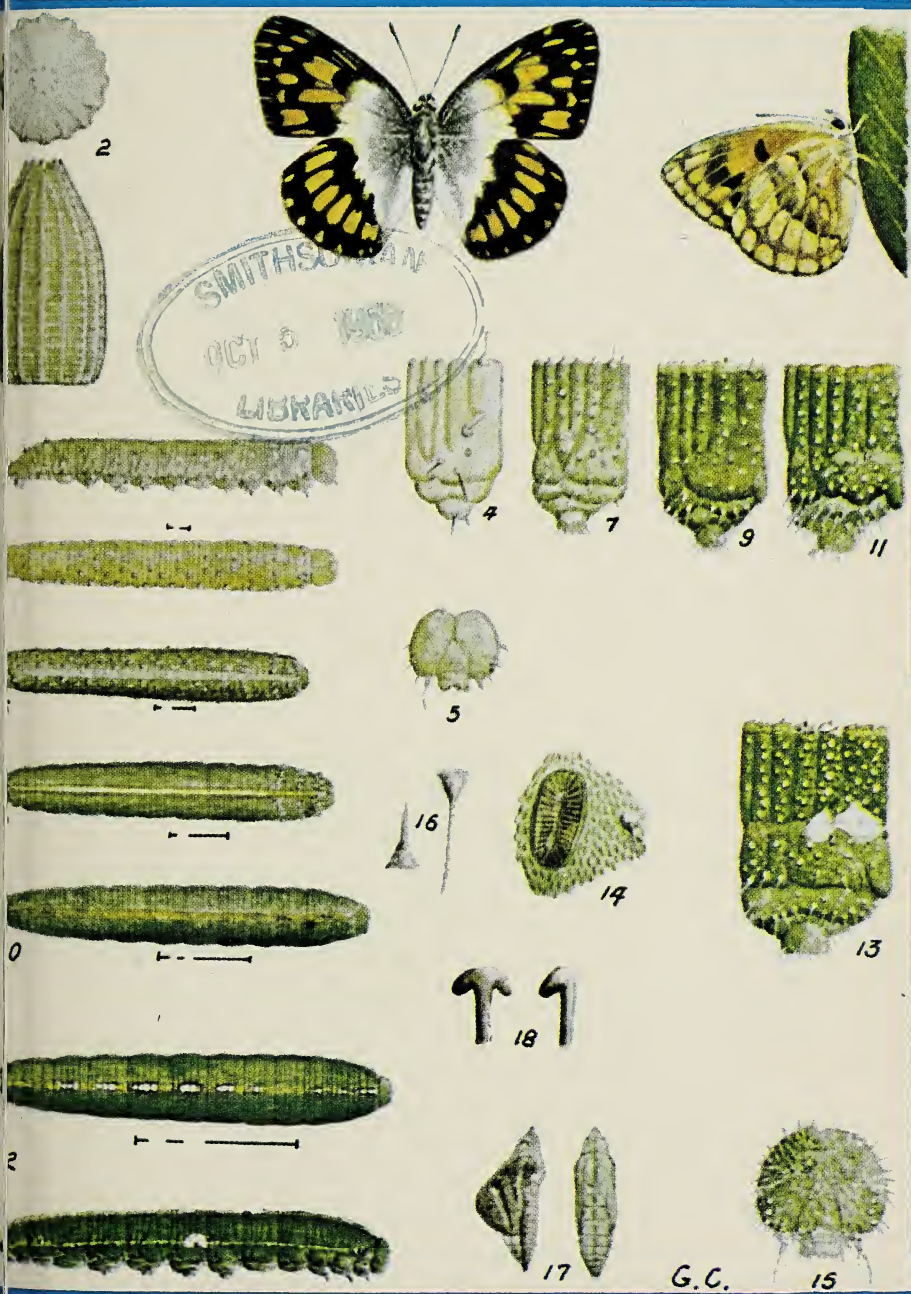
Origin of Autumnal "False Broods" in Common Pierid Butterflies	A. M. Shapiro	181
The Lepidoptera Research Foundation, Inc.		194
Polycrator Polycrator in Mexico	H. A. Freeman	195
Ecological Color Variation in Some Argynnis of the Western United States	W. Hovanitz	197
Natural Habitats	W. Hovanitz	199
Estimating the Density of An Animal Population	William R. Hanson	203

Life History Studies on the <i>Lithosina-Miona-Casta</i> complex of the genus <i>Annaphila</i>	Christopher Henne	249
Studies in the Life Histories of North American Lepidoptera. California <i>Annaphila</i> III.	J. A. Comstock and C. Henne	257
The Generic, Specific and Lower Category Names of the Nearctic butterflies. Pt. 6, The Genus <i>Dryas</i> .	Paddy McHenry	263
A Melanic form of <i>Pieris rapae</i>	J. P. Donahue	266
Man-made Habitat for <i>Colias Eurytheme</i>	W. Hovanitz	267
A New Species of Armyworm — Genus <i>Faronta</i>	J. S. Buckett	268
Early Stages of <i>Lygomorpha regulus</i> .	J. A. Comstock and C. Henne	275
A Previously Unrecognized Subspecies of <i>Philotes</i> <i>speciosa</i> .	J. W. Tilden	281

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28
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OF RESEARCH
ON THE LEPIDOPTERA



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THE PURPOSE OF THE JOURNAL is to combine in one source the work in this field for the aid of students of this group of insects in a way not at present available. THE JOURNAL will attempt to publish primarily only critical and complete papers of an analytical nature, though there will be a limited section devoted to shorter papers and notes. QUALITY WORK on any aspects of research on the Lepidoptera is invited. Analytical and well illustrated works are preferred, with a minimum of long description.

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SPRING MOTHS (MACROHETEROCERA) of a NATURAL AREA IN NORTHEASTERN KANSAS

NOEL McFARLAND

South Australian Museum, Adelaide, South Australia

WHILE ATTENDING THE UNIVERSITY OF KANSAS, between 1958 and 1961, I had the opportunity for considerable (but sporadic) moth-collecting during the spring semesters of 1959, 1960, and 1961. The results are presented in the annotated list that follows. Most of the collecting was restricted to the University of Kansas Natural History Reservation, 7 miles NE of Lawrence, Douglas County, Kansas, at approximately 900 feet elevation. A limited amount of collecting took place in a garden, at one address (1212 Louisiana St.) in Lawrence, Kansas.

BIOTIC DESCRIPTION OF THE RESERVATION

The following is quoted from a paper by Henry S. Fitch (1957) on "The Univ. of Kansas Natural History Reservation — Objectives and Uses": "Natural areas preserving samples of the original flora and fauna in an undisturbed state are almost completely lacking in Kansas; therefore, this reservation created in 1948, will have increasing usefulness and significance as it reverts to an approximation of its original condition, and as other areas that are not protected are further altered by agricultural and industrial uses."

Prior to 1948, the area had been used chiefly for grazing.

The Natural History Reservation, excluding the Rockefeller Tract, covers almost one square mile (590 acres), at elevations between 900 and 1100 feet. Most of the slopes, ravines, and lower areas are heavily wooded, with American elm, oaks, and hickory predominating. Some of the relatively flat hilltops are covered by grassland, and are thought to be remnants of blue-stem prairie, which once dominated larger areas. The habitats represented on the Univ. of Kansas Natural History Reservation have been described in some detail by Fitch (1952, 1958), and by Fitch and McGregor (1956). These papers include not only

descriptions of the Reservation as a whole, but also some detailed descriptions of specific small areas, and a discussion of the past history of the area in general.

For the purposes of this paper, it would be of interest to list (alphabetically) the woody plants growing on the Reservation, as they typify the undisturbed woodland habitat of the area. Of course herbaceous plants (both forbs and grasses) are abundantly represented by numerous species, particularly in the open areas, along roadsides and trails, in disturbed places, around the pond, and in the forest understory. For nearly complete coverage of the higher herbaceous plants (except grasses) of eastern Kansas, see Stevens (1948).

Woody Plants Growing on the Natural History Reservation

(Common species starred; dominant species double-starred)

<i>Acer negundo</i>	<i>Pyrus ioensis</i> **
<i>Ailanthus altissima</i> (scarce)	<i>Quercus macrocarpa</i> (scarce)
<i>Amorpha fruticosa</i>	<i>Q. marilandica</i>
<i>Asimina triloba</i>	<i>Q. muehlenbergii</i> **
<i>Carya ovata</i> **	<i>Q. prinoides</i> *
<i>Celastrus scandens</i> *	<i>Q. rubra</i> (scarce)
<i>Celtis occidentalis</i> *	<i>Q. stellata</i> (scarce)
<i>Cercis canadensis</i> **	<i>Q. velutina</i> *
<i>Cornus asperifolia</i> **	<i>Rhus</i> spp. *
<i>Crataegus mollis</i> **	<i>Ribes</i> sp.
<i>Euonymus</i> sp.	<i>Rosa</i> sp.
<i>Fraxinus americana</i> *	<i>Salix nigra</i> * (at the pond,
<i>Gleditsia triacanthos</i> **	near Reservation head-
<i>Gymnocladus dioica</i> *	quarters, along with three
<i>Juglans nigra</i> *	other <i>Salix</i> spp.)
<i>Juniperus virginiana</i> (the	<i>Sambucus canadensis</i>
only coniferous plant present)	<i>Smilax</i> spp. *
<i>Lonicera</i> sp.	<i>Symphoricarpos orbiculatus</i> **
<i>Maclura pomifera</i> **	<i>Tilia americana</i> (scarce)
<i>Morus rubra</i> *	<i>Ulmus americanus</i> ** (the
<i>Parthenocissus quinquefolia</i> *	commonest tree, but now in
<i>Platanus occidentalis</i> (scarce)	the process of dying off)
<i>Populus deltoides</i>	<i>U. rubra</i>
<i>Prunus americana</i>	<i>Vitis vulpina</i> *
<i>Prunus serotina</i>	<i>Zanthoxylum americanum</i>

Fitch & McGregor (1956) discuss 29 of the above-listed woody plants, with reference to their ecology and occurrence on the Reservation.

TOPOGRAPHY

The collecting station was near the head of a small valley at about 920 feet elevation. Another somewhat larger valley is in the eastern part of the Reservation. The two valleys are separated by a relatively flat hilltop 1040 to 1060 feet in elevation; the hilltop has shallow soil with an underlying layer of hard rock of Pennsylvanian age, the Oread Limestone, and for the most part has a grassland type of vegetation. The slopes between the valleys and hilltop are steep and wooded, with thorny thickets dominated by honey locust, osage orange, and other xeroseral vegetation on the south-facing slopes, but with more mesic woodland including oaks, hickory, and ash, on the north-facing slopes. Much of the woodland is of recent origin, having encroached onto former grassland areas since prairie fires were eliminated.

METHODS OF COLLECTING

Except for the diurnal moths, and those species listed for Lawrence, Kansas, all were collected around the Reservation headquarters buildings, where they were attracted to several 15-watt black lights (ultraviolet tubes — F15T8/BL, without filters). These lights were placed against white walls, or white sheets, about six feet above the ground. No traps were used. Three of the lights faced rather dense woodland edge and streamside habitats, at the south and east edges of a relatively clear area where the buildings stand. Two other lights faced north and northeast toward a rather large, open, grassy field, bordered by woodland. A small pond, with characteristic vegetation, was approximately 200 yards to the northeast.

The lights were turned on sporadically, whenever time was available, during suitable weather from the first mild nights in late March up to the end of May each spring, from 1959 to 1961. On no occasion were the hours between 1 to 5 A.M. sampled. Rarely was it possible to collect on more than three nights per week, and it was not possible to continue this study beyond the end of May each year. It should be emphasized that collecting was restricted to *one* location on the Natural History Reservation. Even though the survey was restricted to this extent, some 226 species of moths were turned up, representing 12 families of the "Macrolepidoptera," and considerable information was gained on the relative abundance of these moths during the spring months.

Collecting in the city of Lawrence turned up a few species that were never encountered at the Reservation; these species are

included in the list, but with the comment "to be looked for at the Natural History Reservation." As might be expected, there were numerous species taken at the Reservation, with its varied native flora, that were never seen in Lawrence.

Extensive daytime collecting at the Reservation was also carried out, during April and May, in favorable weather.

INTRODUCTION TO THE ANNOTATED LIST OF SPECIES

The families follow the arrangement in Part I of the *Check List of Lepidoptera of Canada and the United States of America* by J. McDunnough (1938). The genera and species are arranged *alphabetically*, within each family, for ease of locating the species in this list. (The McDunnough number are included however, at the right margin of the page, opposite the name of the moth). If a question-mark precedes a specific name, this indicates that there is some doubt as to the correct identity of the species; where there is considerable doubt, no specific name is included. Occasional subspecific names are included. In most cases, no mention is made of mere color forms.

Following (1), is given the *flight-period* of the adult, as recorded within the limits of this spring survey. "Early" (preceding the month) indicates the period from the first through the 10th of the month; "mid" indicates the period from the 11th through the 20th; "late" indicates the period from the 21st through the 31st. The word "diurnal" is included, in the few cases where it applies. The last item after (1) is the *abundance-rating* which I have given to the moth, based on its occurrence at the Univ. of Kansas Natural History Reservation during the period of March through May, in 1959, 1960, and 1961. The relative abundance of the moth is expressed by the letter A, B, or C, as follows:

A = abundant.

B+

B = moderate abundance (neither notably common or rare).

B-

C = scarce (6 or fewer records for all three years combined).

C₁ = only *one* record during the entire survey; complete date given.

"B+" (= approaching "A") and "B-" (= approaching "C") are intended to show an inclination either *towards* abundance or scarcity; but the species is still better placed within the "B" category. Little use is made of these "B+" and "B-" ratings, as

they imply rather fine differences in relative abundance, which can hardly be ascertained during a short period of time, with only sporadic and limited collecting. Some of the species placed in the "C" category may actually be commoner, but it would take more (and consistent) collecting to indicate this, if it is the case. Other "C— rated" species are scarce in the spring, as they are just beginning to emerge in late May; but in some cases, these moths become increasingly abundant during June, and perhaps later in the summer. However, in this paper, their abundance-ratings are derived strictly from their occurrence during March, April, and May, and do not imply abundance for the year as a whole. Of course, some of the "C — rated" species are, indeed, truly scarce! But the possible complications should be kept in mind.

There is little likelihood of error with those placed in the "A" category, as this degree of abundance is quite apparent to the collector within a two or three year period at the same locality.

Some of the very earliest species to appear (*i.e.* — late March — April) are single-brooded only, and will not fly again until the following spring. Thus, their flight-periods are completely covered by this survey, and abundance-ratings are probably more accurate for these early species.

Following (2), occasional foodplants are listed, but only when they are known to be the plants eaten by the larvae of these moths at the Univ. of Kansas Natural History Reservation. General information on the foodplants of many of these moths may be found in the writings of Forbes (1920 - 1960), Jones (1951), Crumb (1956), Holland (1905), Peterson (1959), and J. H. Comstock (1950).

Following (3), are *miscellaneous remarks*, which may refer to the adult or to the early stages (*i.e.* — variability; peculiarities in behavior; short notes on the early stages; anything distinctive or worth noting). Under many species, (2) and/or (3) are not included.

MISCELLANEOUS REMARKS

The specimens collected during this spring survey of the Univ. of Kansas Natural History Reservation are chiefly in the author's collection, and in the Snow Entomological Collection, at the University of Kansas. Some are in the Los Angeles County Museum, and in the collection of W. R. Bauer and J. S. Buckett (Davis, California).

The following is a listing of the total numbers of species collected per family:

1. Sphingidae	10	7. Noctuidae	121
2. Citheroniidae	1	8. Notodontidae	18
3. Saturniidae	2	9. Lasiocampidae	2
4. Amatidae	1	10. Drepanidae	1
5. Arctiidae	13	11. Geometridae	55
6. Agaristidae	1	12. Epiplemidæ	1
(TOTAL species		226)	

More extensive and consistent collecting, over a period of several consecutive years (covering all months of the year), and sampling the various habitats on the Reservation, would perhaps bring the total to somewhere between 300 and 400 species of "Macroheterocera." Inclusion of the "Microlepidoptera" would probably add another 200 (or more) species, and inclusion of the butterflies and skippers would probably add another 70 - 80 species to the total for the order Lepidoptera occurring on the Reservation.

It is of interest to note the preponderance of scarce, uncommon, or only moderately common moths in this list. The Reservation is characterized by a moth fauna that is rich in number of species, but relatively few of these species are particularly abundant. This condition is usually seen in undisturbed woodland habitats, where successional changes (in the plant associations) are slow, and the plant species are many; it should become increasingly the case at the Reservation, as it continues to be protected from disturbance. Woodland and forest associations (other than those of mostly coniferous trees) usually have a rich moth fauna, with relatively few of the moths reaching great abundance; this is even more clearly demonstrated in cases where the trees and shrubs are of numerous species, none of which is overwhelmingly common. (Tropical rain forests are an outstanding example of this condition, having *great numbers of species* — both plants and animals — but individuals of most of the species being uncommon or widely-scattered).

The following species (known to occur on the Reservation) have been preserved in the author's collection of preserved early stages of Lepidoptera, and are catalogued under the code-numbers given in parentheses. SPHINGIDAE: *Celerio lineata* (Sp. 4), *Cressonia juglandis* (Sp. 13), *Deidamia inscriptum* (Sp. 1), *Hemaris diffinis* (Sp. 2), *Isogramma hageni* (Sp. 5), *Smerinthus jamaicensis* (Sp. 6); CITHERONIIDAE: *Adelocephala*

bicolor (Ci. 1); SATURNIIDAE: *Actias luna* (St. 1), *Telea polyphemus* (St.2); AMATIDAE: *Scepsis fulvicollis* (Am. 1); LITHOSIIDAE: *Hypoprepia fucosa* (Li. 1); ARCTIIDAE: *Diacrisia virginica* (Ar. 11), *Ecpantheria deflorata* (Ar. 8), *Estigmene acraea* (Ar. 2), *Euchaetias egle* (Ar. 7), *Haploa lecontei* (Ar. 1), *Isia isabella* (Ar. 10); AGARISTIDAE: *Psychomorpha epimensis epimenis* (AS. 1); NOCTUIDAE: *Acronycta obliterata* (N. 20), *Caenurgina crassiuscula* (N. 18), *Catabena lineolata* (N. 11), *Heliothis zea* (N. 4), *Ipimorpha* sp. (N. 27), *Marathyssa inficita* (N. 30), *Orthosia garmani* (N. 26), *O. ? alurina* (N. 2), *Palthis angulalis* ? (N. 57), *Rhodophora gaurae* (N. 16), *Schinia trifascia* (N.15), *Simyra henrici* (N. 22), NOTODONTIDAE: *Cerura* sp. (Nd. 11), *Heterocampa umbrata* (Nd. 3), *Melalopha inclusa* (Nd. 2), *Nadata gibbosa* (Nd. 9), *Schizura ? ipomoeae* (Nd. 13); LASIOCAMPIDAE: *Epicnaptera americana* (La. 4); GEOMETRIDAE: *Abbotana clemataria* (G. 2), *Anavitrinella pampinaria* (G.24), *Biston cognataria* (G. 25), *Calothyssanis amaturaria* (G. 15), *Catopyrrha coloraria* (G. 13), *Palaeacrita vernata* (G. 1), *Plagodis phlogosaria* (G. 33).

Many (but not all) of the above preserved immatures were collected on or near the Natural History Reservation. In most cases, at least the last instar larva was preserved, and for some the complete life history was preserved (all stages and all larval instars).

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THE ANNOTATED LIST OF SPECIES

I. Family SPHINGIDAE

Ampeloeca myron Cram. (1) Late Apr. - May; B (779)

Celerio lineata Fabr. (799) (1) Late Apr. - May; B-

Ceratomia sp. (—) (1) May 13, 1961; C₁

Cressonia juglandis A. and H. (744) (1) Mid-late May; C (2) Juglans nigra (3) Seems to be more abundant in the city of Lawrence than on the Natural History Reservation.

Deidamia inscriptum Harr. (782) (1) Late Apr. - early May; B

(2) Vitis, Parthenocissus (3) This is the earliest and smallest nocturnal sphingid. Most specimens came in at dusk, or just after. The maximum number taken in one evening (at light) was 20 (Apr. 28, 1959). Only three were seen in 1960 (May 2), and none in 1961. The period of flight is short, lasting only about two weeks (at the most), and the moth is only single-brooded. It appears to be quite cyclic from year to year. The larvae were abundant in May 1959, nearly stripping some of the Virginia Creeper vines that climb on tree trunks in the woods. Under these conditions, the larvae did not attempt to hide themselves. They were also common on wild grape, but harder to find by casual searching. A peculiar habit which the larva has (especially when young), is to throw its head clear back, thus pointing the true legs upward; at the same time it usually spits a droplet of fluid. This odd posture is assumed as a reaction to disturbance, and is quite the opposite of the usual sphingiform position.

Hemaris diffinis Bdv. (770) (1) Apr. - May; diurnal only; A

(2) Symphoricarpos orbiculatus, on the Reservation. (3) This is the earliest sphingid. The moth is sometimes attracted to redbud (Cercis) blossoms. The larva bears a caudal horn, like many other sphingids, and also has the general appearance of a "typical" sphingid larva. (fig. 1, photograph of a last instar larva). It has a distinctive mode of locomotion, best described as hesitant, and "forward-inching", which allows it to move inconspicuously along, without drawing much attention to itself. Most of the time, it is quiet, and blends in rather well with the foodplant. The easiest way to obtain Hemaris larvae is to collect the eggs, which are laid singly on the undersides of leaves, as the female moth hovers over the plant. Only an instant is needed for oviposition. Although the foodplant is abundant on the Reservation, the moths show a preference for ovipositing on plants which are in certain types of situations, as follows: (a) single plants, growing in open sunny places, or along roadsides; (b) groups or short rows of plants, growing in sunny clearings in the woods, or at the bases of limestone outcroppings (in the sun). The moths seem to avoid ovipositing on plants that form the shaded understory, where Symphoricarpos grows abundantly beneath trees.

Isogramma hageni Grt. (705) (1) May; A (2) Maclura pomifera

(3) The larvae can be found on Osage orange, in the late summer. They were more common on small trees, out in open grassy fields near the Reservation headquarters. An unusual feature of the larval behavior is that they readily let go of the plant and drop if disturbed; most sphingid larvae hang on tenaciously when disturbed.

- Paonias myops A. and S. (742) (1) Early - mid May; B-
Smerinthus jamaicensis Dry. (739) (1) May 20, 1961; C1 (2) Ulmus americana (3) The single specimen was reared from a larva collected in September, 1960, by Mrs. Fitch, near the Reservation headquarters.
Sphinx ? drupiferarum A. and S. (730) (1) May; B-

II. Family CITHERONIIDAE

- Adelocephala bicolor Harr. (849) (1) Late Apr. - mid May; B+ (2) Gleditsia triacanthos (3) As is the case with quite a few of the moths in this list, a summer brood follows. The first individuals (in spring) have deep gray forewings, whereas most of the summer brood moths have tan (or light golden-brown) forewings; the difference in general appearance is striking.

III. Family SATURNIIDAE

- Actias luna L. (811) (1) Late Apr. - early May; B+ (2) Juglans nigra (3) Fifteen individuals came to light on Apr. 28, 1959; this was a maximum count for any single night.
Telea polyphemus Cram. (812) (1) Late Apr. - May; B (2) Quercus, etc.

IV. Family AMATIDAE

- Scepsis fulvicollis Hbn. (871) (1) May; diurnal and nocturnal; B- (2) Bromus and other grasses (3) Although not common in the spring, it is abundant in Sept., on Solidago blossoms; it is also more common at light in late summer. A larva was collected on Bromus, in Sept., 1960. The hairy larva could be mistaken for an arctiid, but there are no strictly grass-feeding arctiids in this locality.

V. Family ARCTIIDAE

- Apantesis arge Dru. (1038) (1) Late Apr.; C1
Apantesis nais Dru. (1058) (1) May; B
Apantesis phalaerata Harr. (1061) (1) May; A (3) No females were ever taken at the lights. Color and maculation are quite variable on the hindwings, and to a lesser degree on the forewings.
Cycnia ? inopinatus Hy. Edw. (992) (1) May; C
Cycnia tenera Hbn. (991) (1) May; B
Diacrisia virginica Fabr. (= Spilosoma) (1065) (1) Late Apr. May; A (3) This is the first arctiid to appear in the spring.
Estigmene acraea Dru. (1070) (1) May; C
Euchaetias egle Dru. (1001) (1) Late May; larvae were collected in Lawrence (in Sept.) and the adults emerged the following May; to be looked for at the Natural History Reservation (2) on Gonolobus, in Lawrence.
Euchaetias oregonensis Stretch (1005) (1) May; C
Halysidota tessellariis A. and S. (984) (1) May (one specimen collected in Lawrence; to be looked for at the Natural History Reservation).

Haploa lecontei Guer. (1103) (1) Late May; diurnal and nocturnal; B+ (3) The moths are highly variable, from immaculate white to white heavily marked with chocolate-brown on the forewings. The nearly mature larvae are common in early May, especially west of the Rockefeller Tract, where they climb into Ceanothus Ovatus, Symphoricarpos, small box elders, and other plants, to feed and sit in the sun.

Hyphantria cunea Dru. (1075) (1) May; A (3) This species is highly variable in maculation, from immaculate white to heavily-spotted with black. It is the smallest white arctiid in this locality.

Isia isabella A. and S. (1069) (1) May; C (3) This species is more abundant in open fields and roadside habitats, where the familiar hairy larvae (banded in black, rust-brown, and black) are seen crawling over the ground in Sept. - Oct. After overwintering as mature larvae, they spin cocoons in the early spring and emerge in May and June.

VI. Family AGARISTIDAE

Psychomorpha epimenis Dru. (2864) (1) Apr.; diurnal only; B (2) Vitis, Parthenocissus (3) This moth is on the wing just as the buds are beginning to swell and open, in early spring. It is fairly common on mild, sunny days. Although not often inclined to alight, it sometimes comes down to drink on damp or wet ground. Numerous eggs were obtained from a confined female, by feeding her daily and giving her some filtered sunlight each morning, along with sprigs of foodplant. A preference was shown for ovipositing on or under the stipules of the leaves.

VII. Family NOCTUIDAE

Acontia aprica Hbn. (3203) (1) May; C

Acronycta connecta Grt. (1167) (1) Early May; C (3) A melanic specimen was captured.

Acronycta ? hastulifera A. and S. (1149) (1) Early May; C

Acronycta impleta Wlk. (1201) (1) Late Apr. - early May; A (3) As in some other Acronycta spp., melanic individuals are common.

Acronycta longa Gn. (1207) (1) May; B-

Acronycta morula G. and R. (1181) (1) Early May; C (3) This species is much more common in the town of Lawrence.

Acronycta oblinita A. and S. (1215) (1) Mid Apr. - early May; B (3) The bristly, colorful black and yellow larvae are sometimes common on Polygonum (in roadside ditches, etc.) in Sept.

Acronycta paupercula Grt. (1169) (1) Late Apr. - early May; B (3) This species is more common in Lawrence.

Agriopodes teratophora H.-S. (2582) (1) mid - late May; C

Agrotis ypsilon Rott. (1435) (1) Late Apr.; B

Amathes c-nigrum Linn. (1511) (1) May; C

Anagrapha falcigera Kby. (3252) (1) Apr. - mid May; B

Anepia capsularis Gn. (1804) (1) Early - mid May; C

Anorthodes tarda Gn. (2651) (1) May; B-

Argyrostromis anilis Dru. (3458) (1) May; C

Autographa biloba Steph. (3279) (1) May; B (3) This species is more common in Lawrence.

- Baileya australis Grt. (3240) (1) Early - mid May; A
Baileya dormitans Gn. (3241) (1) Early - mid May; C
Baileya ? ophthalmica Gn. (3239) (1) May 2, 1959; C₁
Balsa malana Fitch (2669) (1) May; B+ (3) More common in 1959 than in 1960 or 1961.
Bendis detrahens Wlk. (3527) (1) Early - mid May; C (3) This species is more common in Lawrence.
Bleptina caradrinalis Gn. (3797) (1) May; B (3) This species is more common in Lawrence.
Bomolocha albalienalis Wlk. (3691) (1) Mid May; C
Bomolocha bijugalis Wlk. (3689) (1) Mid - late May; C (3) Sexual dimorphism is noticeable in this species.
Bomolocha sordidula Grt. (3694) (1) Mid May; C
Caenurgina crassiuscula Haw. (3430) (1) Apr. - early May; diurnal and nocturnal; A
Caenurgina erechtea Cram. (3431) (1) Late Apr. - May; diurnal and nocturnal; B-
Catabena lineolata Wlk. (2737) (1) Apr. - early May; C (2) Verbena sp.
Cerastis tenebrifera Wlk. (1495) (1) Early - mid Apr.; B
Cerma cora Hbn. (2559) (1) One collected in Lawrence, May 12, 1961; to be looked for at the Natural History Reservation.
Chamyris cerintha Treit. (3131) (1) One collected in Lawrence, May, 1960; to be looked for at the Natural History Reservation.
Chorizagrotis auxiliaris Grt. (1387) (1) Late Apr. - early May; B
Chytolita morbidalis Gn. (3766) (1) Mid May; C
Cissusa spadix Cram. (3539) (1) Mid-late Apr.; C
Crambodes talidiformis Gn. (2661) (1) Late Apr. - early May; B
Crocigrapta normani Grt. (1950) (1) Apr. - early May; B+ (3) The peak of flight lasts only a week or less.
Delta ramosula Gn. (2589) (1) Mid - late Apr.; C
Diptergia scabriuscula L. (2587) (1) May 12, 1959; C₁
Elaphria festivoides Gn. (2647) (1) May; B
Elaphria grata Hbn. (2650) (1) Late Apr. - May; A
Erastria bellicula Hbn. (3117) (1) May; C
Erastria carneola Gn. (3124) (1) May; B (3) This species is more common in Lawrence.
Erastria muscosula Gn. (3118) (1) Mid - late May; C
Erastria musta G. and R. (3123) (1) May 18, 1959; C₁
Erastria synochitis G. and R. (3120) (1) May; B
Epizeuxis americalis Gn. (3734) (1) Mid May; C (3) May be more common than indicated, as members of this genus are not readily attracted to lights, and they often leave after coming in.
Epizeuxis lubricalis Geyer (3746) (1) Late May; C (3) Adults vary considerably in size.
Eugrotis illapsa Elk. (1483) (1) May; C
Euclidia cuspea Hbn. (3426) (1) May 5, 1960; diurnal only; C₁
 (3) At first glance, the diurnal adult (when on the wing) could be mistaken for a skipper of the genus Erynnis (dusky-wings), but the skippers have a more erratic, darting flight.
Euparthenos nubilus Hbn. (3414) (1) May 11, 1961; C₁
Eupsilia morrisoni Grt. (2305) (1) Mid Feb. - early Apr.; B-
Eutolype electilis form depilis Grt. (—) (1) Mid - late Apr.; B+
 (3) This species was fairly common in 1961, but not in 1959 or 1960.

- Eutolyte grandis Sm. (2194) (1) Late Mr. - early Apr.; B (3) The period of flight lasts only a few nights, but the moth is not uncommon during the limited period that it is on the wing.
- Faronta diffusa Wlk. (1962) (1) Late Apr. - early May; B
- Galgula partita Gn. (2666) (1) Apr. - May; B (3) This species is more common in Lawrence. Its color is quite variable, from pale tan to rich, dark brown.
- Heliothis zea Boddie (corn-ear worm) (2932) (1) May; C
- Himella intractata Morr. (1840) (1) Early - mid Apr.; B
- Homohadena infixa Wlk. (2153) (1) May 28, 1959; C₁
- Homorthodes lindseyi Benj. (1890b) (1) May 18, 1959; C₁
- Hypena humuli Harr. (3706) (1) Early - mid Apr.; C
- Hypsorophora hormos Hbn. (3611) (1) One collected in Lawrence, May 26, 1959; to be looked for at the Natural History Reservation.
- Isogona tenuis Grt. (3643) (1) Mid - late May; B-
- Lacinipolia anguina Grt. (1716) (1) Mid May; C
- Lacinipolia renigera Steph. (1738) (1) May; B (3) Although common in 1959, it was scarce in 1960 and 1961.
- Lascoria ambigualis Wlk. (3805) (1) May; C (3) Sexual dimorphism is notable; the male has a cleft forewing, but the female does not.
- Legna perditalis Wlk. (3685) (1) One collected in Lawrence, May 25, 1959; to be looked for at the Natural History Reservation.
- Leucania phragmitidicola Gn. (1978) (1) May, especially early May; B-
- Leucania ursula Fbs. (1974) (1) May; B
- Leuconycta diphteroides form obliterata Grt. (2576) (1) Mid - late May; C
- Lithophane antennata Wlk. (2242) (1) Apr. 6, 1960; C₁
- Marathyssa inficita Wlk. (3223) (1) May 13, 1960; C₁ (2) Rhus trilobata
- Matigramma pulverilinea Grt. (3506) (1) Mid May; C
- Melipotis indomita Wlk. (3549) (1) May 23, 1960; C₁
- Melipotis jucunda Hbn. (3551) (1) One collected in Lawrence, mid May, 1960; to be looked for at the Natural History Reservation.
- Mocis texana Morr. (3435) (1) May; B
- Morrisonia confusa Hbn. (1904) (1) Apr. - early May; C
- Morrisonia distincta Hbn. (1671) (1) Late Apr. - early May; B+
- Neoerastris apicosa Haw. (3126) (1) May 18, 1959; C₁
- Ogdoconta cinereola Gn. (2773) (1) May; C
- Orthodes crenulata Butl. (1871) (1) May 18, 1959; C₁
- Orthosia alurina Sm. (1941) (1) Apr.; A
- Orthosia garmani Grt. (1938) (1) Early - mid Apr.; A (3) The flight period is extremely short, with the moths at a "peak" for only one or two nights, at which time they are abundant. Largest numbers were seen on April 4, 5, and 6, 1959 and April 11, 1960. Larvae, reared from eggs, proved to be general feeders on various woody plants, including Ulmus and Cornus.
- Orthosia hibisci Gn. (1943) (1) Apr.; A
- Orthosia rubescens Wlk. (1937) (1) Apr.; B-
- Palthis angulalis Hbn. (3807) (1) May; B (3) This species is more common in Lawrence. At the Natural History Reservation, larvae (Sept. - Oct.) are feeding on the dead, dried, papery seed capsules of Lobelia syphilitica, which they closely match in coloration. The larvae are quite inactive, and slow in their movements, resting quietly on the stem below the empty seed capsule, or on

the capsule itself. They are multiple-brooded, and have been recorded from many other foodplants. See Comstock and McFarland (1961).

- Panopoda carneicosta Gn. (3535) (1) May 28, 1959; C₁
Panopoda refimargo Hbn. (3534) (1) May 21, 1960; C₁ (3) As is the case with quite a few of the moths listed for late May only, P. rufimargo is barely represented as its flight is just starting, but it becomes more abundant in June.
Parallelia bistriaris Hbn. (3422) (1) One collected in Lawrence, mid-May, 1959; to be looked for at the Natural History Reservation.
Peridroma margaritosa Haw. (1946) (1) Late Apr. - early May; B+
Perigea xanthioides Gn. (2610) (1) Mid May; C
Phalaenophana pyramusalis Wlk. (3750) (1) May; C
Phalaenostola larentioides Grt. (3769) (1) May 28, 1959; C₁
Phipposopus callitrichoides Grt. (3639) (1) May 24, 1961; C₁
Phoberia atomaris Hbn. (3545) (1) Late Mar. - mid Apr.; A
Phosphila miselioides Gn. (2549) (1) Mid - late May; C
Plathypena scabra Fabr. (3705) (1) Mid May; B
Platysenta vecors Gn. (2620) (1) Late Apr. - early May; B
Platysenta videns Gn. (2613) (1) Apr. - May; B+
Plusia aerea Hbn. (3296) (1) One collected in Lawrence, May 25, 1959; to be looked for at the Natural History Reservation.
Plusiodonta compressipalpis Gn. (3612) (1) Late Apr. - early May; B (3) This moth is more common in Lawrence.
Polia adjuncta Bdv. (1691) (1) May 23, 1960; C₁
Prodenia ornithogalli Gn. (2678) (1) Late Apr. - early May; C
Proxenus miranda Grt. (2662) (1) Mid - late May; B (3) The forewings have a distinct glossy sheen.
Psaphida grotei Morr. (2191) (1) Early - mid Apr.; B
Pseudaletia unipuncta Haw. (1994) (1) Late Apr. - May; A
Psychomorpha epimenis (see AGARISTIDAE)
Pyrria umbra Hufn. (2715) (1) A few collected in Lawrence, late May; to be looked for at the Natural History Reservation.
Raphia abrupta Grt. (1140) (1) Late Apr. - mid May; B+
Salia interpuncta Grt. (3731) (1) May 11, 1961; C₁
Sericaglaea signata French (2298) (1) Mid - late Apr.; C
Simyra henrici Grt. (1222) (1) Late Apr.; C (3) One of the colorful, early larvae was collected on Sorghum, in a roadside ditch (early Oct.).
Spiloloma lunilinea Grt. (3595) (1) Mid - late May; B-
Stiriodes obtusa H.-Sch. (2832) (1) May 28, 1959; C₁
Tarachidia candefacta Hbn. (3176) (1) Mid May; C
Tarachidia erastrionides Gn. (3172) (1) Mid - late May; B
Trachea delicata Grt. (2547) (1) May 11, 1961; C₁ (3) The forewings are marked with olive green, which often discolors in the killing jar.
Trichoplusia ni brassicae Hbn. (3269) (1) Late Apr. - early May; C
Ulolonche culea Gn. (1831) (1) May; C
Xanthoptera nigrofimbria Gn. (3113) (1) Mid - late May; B- (3) As is the case with some of the other species listed, this moth is abundant later in the year, although uncommon in its spring brood.
Zale galbanata Morr. (3478) (1) Apr. - May; C
Zale ? minerea Gn. (3484) (1) Late May; C
Zanclognatha cruralis Gn. (3762) (1) Collected in Lawrence, mid-late May; to be looked for at the Natural History Reservation.

VIII. Family NOTODONTIDAE

- Dasylophia anguina A. and S. (3880) (1) May 13, 1960; C₁
Gluphisia septentrionalis Wlk. (3939) (1) May; B-
Heterocampa bilineata Pack. (3908) (1) May; C
Heterocampa guttivitta Wlk. (3907) (1) Early - mid May; C
Heterocampa sp. (—) (1) May 23, 1959; C₁
Heterocampa umbrata Wlk. (3902) (1) May 29, 1960; C₁ (3) This single record is from a pupa, collected under a log (Oct.), about 5 mi. WSW of the Natural History Reservation. A female emerged on the date given above.
Hyperaeschra georgica H.-S. (3845) (1) May 14, 1959; C₁
Lophodonta angulosa A. and S. (3854) (1) One collected in Lawrence, late May; to be looked for at the Natural History Reservation.
Melalopha albosigma Fitch (= Ichthyura a.) (3827) (1) Mid Apr. early May; B
Melalopha apicalis Wlk. (3822) (1) May 4, 1959; C₁
Melalopha inclusa Hbn. (3825) (1) Early - mid May; B (3) A number of larvae were collected on Populus (in Sept.), near the Reservation headquarters; these emerged in May, 1961. The larvae are gregarious, in a web-nest of two or more leaves.
Misogada unicolor Pack. (3909) (1) Mid May; C
Nadata gibbosa A. and S. (3857) (1) May 11, 1961; C₁ (3) This moth was often seen in Lawrence.
Nerice bidentata Wlk. (3858) (1) Late Apr. - early May; B+ (3) The period of flight is rather short.
Oligocentria lignicolor Wlk. (3912) (1) May; C
Schizura apicalis G. and R. (3926) (1) Mid - late May; C
Schizura ipomoeae Dbldy. (3920) (1) May 21, 1960; C₁
Schizura unicornis A. and S. (3924) (1) Late Apr. - mid May; C

IX. Family LASIOCAMPIDAE

- Epicnaptera americana Harr. (3999) (1) Apr. - early May; B
Heteropacha rileyana Harv. (3998) (1) Apr.; B+ (3) The peak of abundance lasts only a few nights. Only two or three females came to the lights during the entire survey.

X. Family DREPANIDAE

- Eudeilinea herminiata Gn. (4017) (1) May; C (3) There are pure white geometrids for which this moth could be mistaken.

XI. Family GEOMETRIDAE

- Abbotana clemataria A. and S. (5199) (1) Apr. - early May; B+ (2) Fraxinus, etc. (fig. 2, photograph of a last instar larva).
Anacamptodes defectaria Gn. (4915) (1) Mid - late Apr.; C
Anavitrinella pampinaria Gn. (4908) (1) Late Apr. - May; A
Apicia confusaria Hbn. (5184) (1) Fairly common during mid - late May, in Lawrence; to be looked for at the Natural History Reservation.
Bapta vestaliata Gn. (4606) (1) Late Apr. - May; diurnal and nocturnal; B+ (3) As this small geometrid is pure, shining white, it is very conspicuous when flying in the daytime.

- Biston cognataria Gn. (4968) (1) May 24, 1961; C₁
Calothysanis amaturaria Wlk. (4205) (1) Mid - late May; B-
(2) Rumex crispus (3) The very unusual dark brown larvae are considerably swollen in the thoracic region. They make no attempt to hide on their foodplant, and are easily collected by searching.
Catopyrrha coloraria Fabr. (4642) (1) Late Apr. - mid May; diurnal and perhaps nocturnal; B+ (2) Ceanothus ovatus (3) This moth was encountered only in a grassland-field, directly NW of the Natural History Reservation, in places where Ceanothus was growing amongst the grasses. In this restricted habitat, for a short period, it was rather common. The moth rests on the ground, with its wings up over its back. It flies up when approached, but lands again, a short distance away. The behavior is reminiscent of Sericosema spp. A large number of larvae were reared from eggs in 1961. Although offered many different plants from the habitat, they accepted only Ceanothus.
Chlorochlamys chloroleucaria Gn. (4095) (1) Late Apr. - mid May; B
Cleora sublunaria Gn. (4876) (1) Apr. - mid May; A
Coryphista meadi Pack. (4248) (1) Two records for early May, 1959, in Lawrence; the moth might occasionally turn up at the Natural History Reservation, although its only recorded foodplant is Berberis (=Mahonia).
Deilinia quadrifasciaria Pack. (4611) (1) May 28, 1959; C₁
Dichorda iridaria Gn. (4082) (1) May; C
Dyspteris abortivaria H.-S. (4234) (1) May; B-
Ectropis crepuscularia Schiff. (4946) (1) Mid Apr. - early May; B
Enconista dislocaria Pack. (= "Semiothisa" d.) (4703) (1) Late Apr. - early May; B
Euacidalia sericeata Pack. (4109) (1) Mid - late Apr.; C (3) This is the smallest spring geometrid collected on the Natural History Reservation.
Euchlaena pectinaria D. and S. (5003) (1) Late Apr. - mid May; C
Eugonobapta nivosaria Gn. (4991) (1) May; C (3) This moth is of the same size and color as Eudeilinea herminiata Gn., a drepanid, which also occurs on the Natural History Reservation.
Eumacaria latiferrugata Wlk. (= Itame l.) (4774) (1) Mid Apr. mid May; C
Euphyia centrostrigaria Woll. (4559) (1) Late Apr. - May; B
Eupithecia herefordaria C. and S. (4310) (1) Apr. - May; B+
Eupithecia swetti Grossb. (4354) (1) Apr. - May; B
Haematopis grataria Fabr. (4204) (1) Collected during May, in Lawrence; to be looked for at the Natural History Reservation.
(3) Remarks under Xanthoptera nigrofimbria (Noctuidae) apply here, as well as to a number of the other geometrids listed.
Heterophleps refusata Wlk. (4231) (1) May; C
Heterophleps triguttaria H.-S. (4233) (1) Mid - late May; C
Horisme intestinata Gn. (4393) (1) Abundant in Lawrence, in mid to late May; to be looked for at the Natural History Reservation.
Hydriomena pluviala Gn. (4477) (1) One collected in Lawrence, Apr. 26, 1960; to be looked for at the Natural History Reservation.
Hyperetis amicararia H.-Sch. (5043) (1) Late Apr. - May; B-
Lobocleta ossularia Hbn. (4115) (1) One collected in Lawrence, in mid May; to be looked for at the Natural History Reservation.

- Lycia ypsilon S. A. Forbes (4952) (1) Apr.; A (3) The moth reaches a peak of considerable abundance in one or two nights, and then rapidly disappears until the following April. On Apr. 6, 1959, over 200 individuals came to one light. No females were ever taken at the lights.
- Melanolophia signataria signataria Wlk. (4857) (1) Apr. - early May; A (3) The maculation is somewhat variable.
- Mellilla xanthometata Wlk. (4657) (1) Apr. - May; sometimes on the wing in the daytime, although primarily nocturnal; A
- Metanema inatomaria Gn. (5054) (1) Mid - late May; C
- Metarranthis duaria Gn. (5050) (1) Early - mid May; C (3) This moth may be more common than indicated, as individuals have a tendency to leave the immediate vicinity of the light after once flying in.
- Metarranthis ? homuraria Grt. (5046b) (1) Mid May; C
- Palaeacrita merriccata Dyar (4961) (1) Early Apr.; C
- Palaeacrita vernata Peck (4960) (1) Jan. - Mar. - Apr. - mid May; A+ (2) Ulmus americanus, U. rubra, etc. (3) The males occasionally come to lights (on mild nights) in Jan. and Feb., and they become extremely abundant in March and April. Periodically, the larvae of this moth defoliate the elms, shortly after they leaf out, but the trees usually recover (with a secondary crop of leaves) by late May, at which time the larvae have dropped to the ground to pupate.
- Percnoptilota obstipata Fabr. (4535) (1) Mid Apr. - May; B- (3) Sexual dimorphism is notable.
- Pero ? honestarius Wlk. (5072) (1) Apr. - early May; B
- Phigalia olivacearia Morr. (4956) (1) Apr. (particularly early Apr.); B
- Phigalia titea Cram. (4958) (1) Apr. (particularly early Apr.); A
- Philobia aemulataria Wlk. (4665) (1) Late Apr. - early May; B
- Plagodis phlogosaria Gn. (a spring form) (5040) (1) Late Apr. - mid May; C
- Scopula inductata Gn. (4158) (1) Mid - late May; C
- Scopula limboundata Haw — (1) Mid - late May; B (3) The maculation is variable.
- Semiothisa continuata Wlk. (4710) (1) May; C
- Semiothisa gnophosaria Gn. (4738) (1) Mid - late May; C
- Semiothisa ocellinata Gn. (4723) (1) May; C
- Synchlora aerata Fabr. (4070) (1) Two specimens collected in Lawrence, in late May; to be looked for at the Natural History Reservation.
- Tetracis crocallata Gn. (5197) (1) Mid - late May; B
- Tornos abjectarius calcasia C. and S. (—) (1) Mid Apr. - mid May; B-
- Tornos scolopacinarius scolopacinarius Gn. (4812) (1) Mid Apr. - mid May; B
- Xanthotype ? sospeta Dru. (5007) (1) Mid - late May; B- (3) This moth is more common in Lawrence, although not abundant.
- Xystrota rubromarginaria Pack. (4134) (1) Apr. - mid May; diurnal and nocturnal; A (3) This is a common diurnal spring geometrid on the Reservation, but it also comes to lights after dark.

XII. Family EPIPLEMIDAE

- Callizzia amorata Pack. (5223) (1) May; C

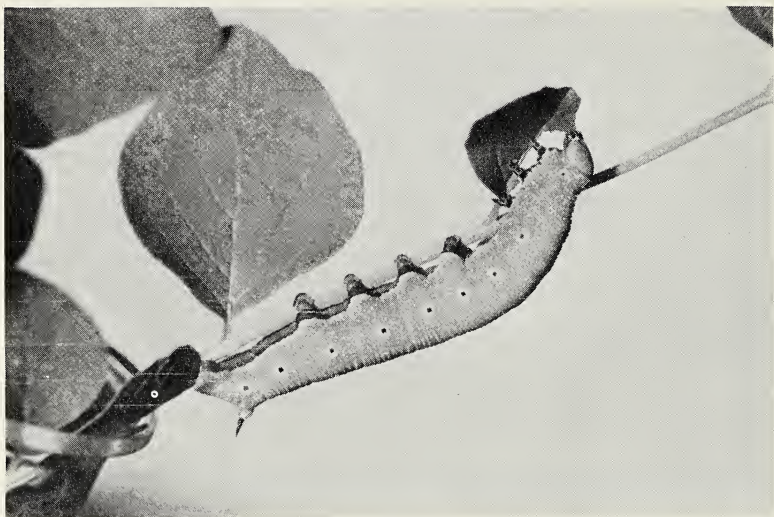


Fig. 1—*Hemaris diffinis* (last instar, alive and feeding) on foodplant, *Symphoricarpos orbiculatus*. Univ. Kansas Nat. Hist. Res., 7 mi. N.E. Lawrence, Douglas Co., Kansas. May, 1960. Reared from egg.

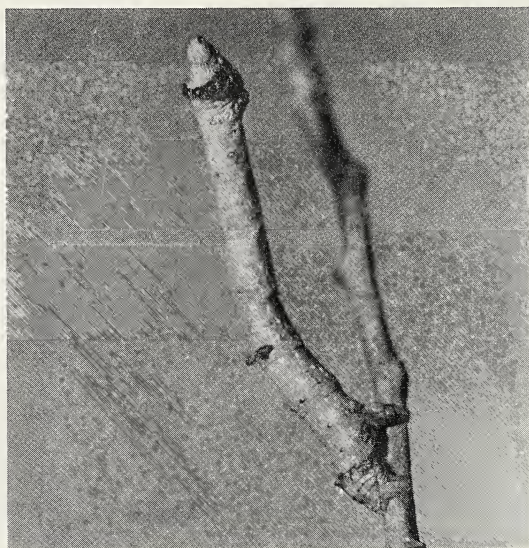


Fig. 2—*Abbotana clemataria* (Geometridae), last larval instar, alive. Reared from egg on *Fraxinus* at Lawrence, Douglas Co., Kansas. A general feeder on many trees and shrubs.

A NEW SPECIES OF *NEPTICULA* ON BUR OAK IN ONTARIO (*NEPTICULIDAE*)

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DURING THE PAST FEW YEARS some officers of the Forest Insect Survey of Canada, Department of Forestry and Rural Development, have been studying an undescribed species of *Nepticula* v. Heyd. which is abundant on bur oak in the Lake Simcoe District of Ontario. The description is presented here to assist those officers in publishing the results of their investigations.

Nepticula macrocarpae sp. n.

General. Face black. Vertex creamy yellow. Antenna blackish at base, gradually becoming ochreous toward apex. Eye-cap, thorax, base of fore wing, and median wing fascia creamy yellow. Median fascia broad, occupying about one-third of wing just before middle, and slightly wider on coastal and trailing margins. Remainder of wing brownish-black; apical fringe whitish; trailing fringe fuscous. Hind wing and fringe fuscous. Abdomen dull steel-grey dorsally, creamy yellow ventrally. Legs creamy yellow. Wing spread 4 mm. There are two generations each year. The moths occur in early June, and again in late July and early August.

Male genitalia (Fig. 1). Uncus heavily sclerotized, bilobed. Gnathos heavily sclerotized, M-shaped. Vinculum broadly arcuate laterally, truncate ventrally. Clasper broad, with apical tooth. Transtilla bifid, each arm subtriangular. Aedeagus broad, short, tubular; cornutus broad, arcuate.

Female genitalia (Fig. 2). Ovipositor lobes short, subconical. Apophyses short, thick. Ductus bursae membranous. Bursa with two bands of short stout teeth.

Mine. Upper side serpentine, about 2 cm. long and with a central frass line.

Holotype. Male, Orillia, Ontario, 12 August 1965. Forest Insect Survey No. S65-4100-01. No 9539 in the Canadian National Collection, Ottawa.

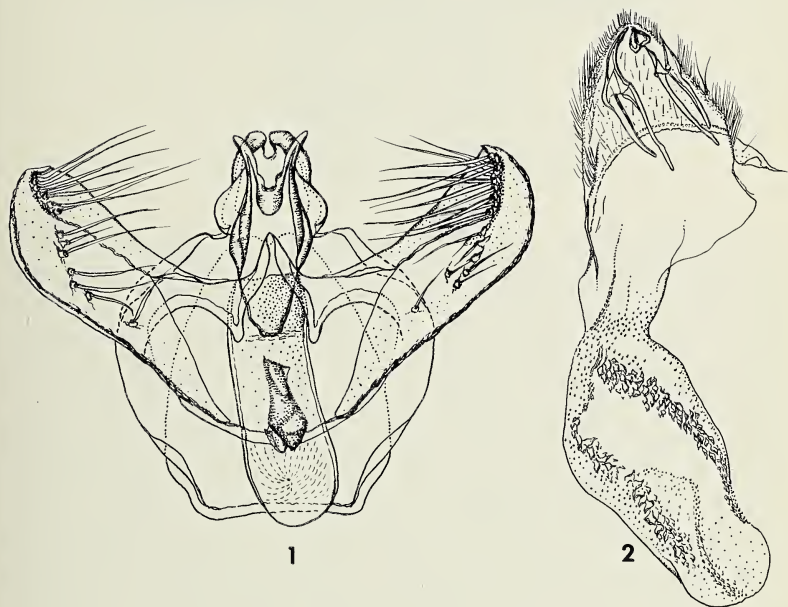
Paratypes. Seven males, thirteen females, same locality as holotype, August 12, 15, 30, 1965. All type material reared from *Quercus macrocarpa* Michx.

Distribution. Known only from Orillia, Ontario, but probably occurs elsewhere within the distribution of the host tree.

Remarks. This species will key to *latifasciella* Chambers in Braun's key in Forbes (1923, *Cornell Univ. Agr. Exp. Sta. Mem.* 68: 84). I have examined Chambers' type in the Museum of Comparative Zoology, Cambridge, Mass. It is a female securely glued to a paper point, and except for the thorax, is in good condition. There are several differences between it and *macrocarpae*. Firstly, Chambers collected his specimen in Kentucky from the bark of a sweet chestnut tree (*Castanea dentata* (Marsh.) Borkh.), the leaves of which contained many empty *Nepticula* mines. Secondly, there are significant colour differences as outlined below.

N. latifasciella. Face rusty-yellow. Vertex dark brown. Antenna silvery. Abdomen fuscous dorsally, pale greyish fuscous ventrally. Legs dark fuscous.

N. macrocarpae. Face black. Vertex creamy yellow. Antenna blackish basally, ochreous apically. Abdomen steel-grey dorsally, creamy yellow ventrally. Legs creamy yellow.



Figs. 1, 2.—Genitalia of *Nepticula macrocarpae* sp. n. 1, male. 2, female.

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FIXATION OF THE TYPE LOCALITY OF *LYCAENA PHLAEAS HYPOPHLAEAS* (BOISDUVAL) AND A FOODPLANT CORRECTION

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C. F. DOS PASSOS (IN LITT.) POINTED OUT that the type locality of *Lycaena phlaeas hypophlaeas* listed as "north of California" (J. Res. Lep. 5: 231) should instead be translated "Northern California." The type(s) was collected by P. J. M. Lorquin in 1852. Lorquin's California explorations appear in a mimeographed pamphlet, "Pierre Joseph Michel Lorquin — Naturalist-voyageur," by Estelle H. Lorquin, published by the Lorquin Service in San Francisco in 1938. L. M. Martin (per. communication) of the Los Angeles County Museum determined where Lorquin collected during 1952-1853 in relation to the pamphlet text. During that time, Lorquin "explored at first all the neighborhood of San Francisco, then the banks of the Sacramento and Plumas rivers; made trips in the Sierra Nevada chain, and ventured as far as the great forests of the interior." In view of what is known about the California distribution of *hypophlaeas*, the probable type locality is the Sierra Nevada Mountains, California. F. M. Brown (in litt.) says that the type locality could well have been the gold region in Tuolumne County.

T. Iwase pointed out (in litt.) that the record of daikon by Yokoyama as a foodplant for *Lycaena phlaeas daimio* in Japan was a misprint. He says there are five foodplants recorded in Japan: *Rumex japonicus*, *R. acetosa*, *R. acetosella*, *R. obtusifolius*, and *R. domesticus*. Thus the known foodplants for *L. phlaeas* subspecies are all in Polygonaceae—daikon (*Raphanus*) previously being the only exception.

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DESCRIPTION OF A NEW SPECIES OF *XYLOMIGES* FROM CALIFORNIA

WITH NOTES AND ILLUSTRATIONS

(LEPIDOPTERA: NOCTUIDAE: HADENINAE)

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IT IS MY PLEASURE at this time to present a description of an undescribed noctuid species of the genus *Xylomiges* Guenee. This species has been in the Bauer-Buckett collection for well over ten years now, and in the interim many specimens have accumulated. This species has a peculiar flight habit, and because of this characteristic, males of the species were never taken until relatively recent times. The females come out in the evenings, usually between 7:30 P.M. and 8:00 P.M., and can be secured until 10:00 P.M. on normal nights. The males have never been taken before 10:00 P.M., and become abundant about 11:00 P.M. and later on normal occasions. The temperatures along the coast are cool in the early part of the year (January and February), and the humidity is very high, and therefore, collectors seldom would stay out until 10:00 P.M. collecting. Because of this factor, males were never taken until recently when colleagues and I remained out all night collecting.

The type locality is a typical coastal Pine belt vegetation, the dominant tree being Bishop Pine (*Pinus muricata* Don.). Madrone (*Arbusus menziesii* Pursh.), Tanbark (*Lithocarpus densiflorus* (H. & A.)), California Laurel (*Umbellularia californica* (H. & A.)), and Coast Live Oak (*Quercus agrifolia* (Nee.)), are other common trees of the area. Common shrubs of the area are various species of *Ceanothus*, Coyote bush (*Baccharis pilularis* DC.), Manzanita (*Arctostaphylos* spp.), Huckleberry



Fig. 1—Map depicting the distribution of *Xylomiges baueri* Buckett and *X. variabilis* (Smith). Note the restricted distribution of *baueri*.

(*Vaccinium* spp.), and Salmon-berry (*Rubus spectabilis* Pursh.). Many other smaller herbaceous plants abound also. While in the company of Mr. Bill Bauer and Mr. Chris Henne, search for the eggs and larvae was done. The only larva we found that resembled one of the *Xylomiges* species was one found in the tip of staminate cone of a young Bishop Pine. The larva was in an intermediate instar, and as yet has not emerged (according to Mr. Chris Henne who is rearing the specimen). It seems probable that Bishop Pine will prove to be the host plant of this new species. *Xylomiges variabilis* Smith, the closest relative to *Xylomiges baueri* n. sp., is a pine feeder, and thus, this is the reason for suspecting Bishop Pine in this case.

XYLOMIGES BAUERI n. sp.

Male: Ground color of primaries dorsally maroon, secondaries dorsally with pink tint. Head with vertex clothed in tricolor, elongate hairs, basally brown, subapically maroon, apically white-tipped; frons clothed as in vertex, for most part, but with more maroon elongate hairs; maxillary palpi exterolaterally brownish, ventrally possessing elongate white-tipped maroon hairs; proboscis normal; eyes very hairy; antennae with scape and pedicel clothed in whitish and maroon scales and hairs; flagellomeres bipectinate-fasciculate, pectinations becoming shorter apically, terminally ciliate. Thorax with collar maroon, composed of elongate white-tipped hairs; disc and tegulae clothed in brown, maroon, white-tipped dentate hairs; ventrally clothed in maroon and whitish elongate hairs; tarsi black and white banded; unguis very weakly bifid; primaries dorsally maroon; basal line bicolor, basally black, apically irrorated with white scales so as to appear grey, or blue-grey; transverse anterior line uneven in course, bicolor, basally blue-grey, apically black; median area blackish on inner margin, remainder maroon; orbicular squarish, grey, centrally blackish, outlined with light colored scales, anastomosing with reniform; reniform centrally maroon, outlined in creamy scales; transverse posterior line undulating, represented as line of demarcation between median and subterminal areas; subterminal area bicolor, basally grey, apically cream yellowish; subterminal line jagged, represented as line of demarcation between cream yellow coloration and grey terminal area; terminal area with transverse black dashes on veins; fringes composed of spatulate white-tipped scales, alternating maroon and brown from apex to point of inner margin, or tornus; inner margin basally and medially with



Fig. 2—Holotype male, *Xylomiges baueri*. Inverness, Marin County, California, 6 February 1965 (J. S. Buckett).

Fig. 3—Allotype female, *X. baueri*. Same locality as holotype, 2 February 1962 (J. S. Buckett and G. M. Trenam).

fringe of elongate maroon hairs; ventral surface dark, dusky, costally and apically, basally dirty white, overlain with tint of maroon; dark spot present in area of reniform; secondaries dorsally with pink tint; discal dot dusky, prominent; terminal line dusky; veins slightly outlined in fuscous; fringes a pinkish-maroon; ventral surface pinkish basally; remainder of surface a dirty white, overlain with hue of rose-colored scales; discal dot prominent; suggestion of exterior line, fuscous; a short, faint band of fuscous scales running parallel to exterior line innermarginally; fringes pinkish. Abdomen clothed both dorsally and ventrally in brown and rose colored elongate hairs and paucity of scales. Greatest expanse of forewing \pm 16mm. Genitalia as in figures 4 and 5.

Female: As in male, very little variation, except somewhat larger; antennae ciliate, rather than as in male. Greatest expanse of forewing \pm 18 mm. Genitalia as in figure 6.

SPECIMENS EXAMINED

CALIFORNIA: Holotype male, Inverness, Marin County, 6 February 1965 (J. S. Buckett). Paratypes: 1 female, (designated allotype), Inverness, Marin County, 2 February 1962 (J.S.B. & G. M. Trenam); remainder of paratypes all from Inverness, Marin County, unless otherwise stated; 1 female, 14 February 1950 (W. R. Bauer); 1 female, 14 February 1955 (W.R.B. & J.S.B.); 1 female 31 January 1956 (W.R.B. & J.S.B.); 1 female, 16 February 1960 (W.R.B. & J.S.B.); 1 female, 31 January 1961 (J.S.B.); 1 female, 1 February 1961 (J.S.B.); 2 females, 4 February 1961 (W.R.B. & J.S.B.); 3 males, 3 females, 1 February 1962 (J.S.B. & G.M.T.); 10 males, 6 females 2 February 1962 (J.S.B. & G.M.T.); 4 females, Tomales Bay State Park, Marin County, 6 February 1960 (W.R.B. & J.S.B.); 1 male, Mendocino, Mendocino County, 28 November 1959 (J. R. Helfer).

Holotype deposited in the Type Collection, Department of Entomology, University of California, Davis. Allotype female deposited in the Bauer-Buckett Collection, Davis, California. Remainder of paratypes deposited in the following institutions and collections: American Museum of Natural History, New York; Bauer-Buckett Collection, Davis; California Academy of Sciences, San Francisco; California Department of Agriculture, Sacramento; Franclemont Collection, Ithaca, New York; Los Angeles County Museum of Natural History; United States National Museum, Washington, D.C.; University of California, Berkeley and Davis.

There is also a large series of *Xylomiges baueri* contained in the Franclemont Collection, Cornell University, Ithaca, New York, which was unavailable for study at this time. The specimens of this large series were collected at the same localities as these listed in the "specimens examined" section of the present



4



5

Fig. 4—Paratype, *Xylomiges baueri*. Male genitalia minus aedeagus. Inverness, Marin County, California, 3 February 1962 (J. S. Buckett and G. M. Trenam), Bauer-Buckett Slide No. 65D2-4.

Fig. 5—Paratype, *Xylomiges baueri*. Male aedeagus. Data same as in fig. 4.



Fig. 6—Paratype, *Xylomiges baueri*. Female genitalia. Locality and collectors same as in fig. 4, 11 February 1962, Bauer-Buckett Slide No. 65D1-2.

work (primarily at Inverness, Marin County), and were collected by the author and colleagues.

Xylomiges baueri is most closely related to *X. variabilis*, as is evidenced by both the male and female genitalia, as well as by maculation of the primaries. In distribution, *baueri* is thus far known to occur in the Central California coastal area, particularly immediately adjacent to the ocean. In the past, *baueri* has not been collected over one air mile from the ocean. This restricted distribution is, no doubt, due to the confined range of its probable host plant, Bishop Pine.

Xylomiges variabilis is not particularly restricted in distribution, as is *baueri*, and it occurs throughout much of the western United States, and at higher elevations (see distribution map). In the Bauer-Buckett collection specimens of *variabilis* are represented from the following localities: Arizona: Madera Canyon, Santa Cruz County. California: Alturas, Modoc County; Benton Station, Mono County; Bishop, Inyo county; Cobb Mountain, 8 miles northwest of Middleton, Lake County; Fish Camp, Madera County; Johnsville, Plumas County; Markleville, Alpine County; Mohawk, Plumas County; Pinyon Crest, Riverside County; Valyermo, Los Angeles County. Utah: Dividend, Utah County; Eureka, Juab County; Provo, Utah County. Due to the distribution of both species, it seems more probable that *variabilis* was an earlier occurring species evolutionarily speaking, and that it could have even given rise to *baueri*.

Mr. William R. Bauer of this Bureau was the first person known to discover this undescribed entity, and therefore, I take great pleasure in naming it in his honor.

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THE LIFE-HISTORIES OF SOUTH AFRICAN *COLOTIS ERONE*, *C. IONE*, *C. VESTA* AND *LEPTOSIA ALCESTA* (PIERIDAE)

THE LATE GOWAN C. CLARK AND C. G. C. DICKSON¹

Cape Town, South Africa

THE EARLY STAGES of two of these very beautiful Pierids were recorded in full, comparatively recently, apparently for the first time, and they are now being described and illustrated in colour in the present paper.

The first species, *Colotis erone* (Angus), was reared from eggs and larvae procured by the second writer at Umhlanga Rocks, Natal, in 1955 and 1956, and the other species, *Colotis ione* (Godart), from eggs laid by a captive female caught by Mr. T. W. Schofield at the Shongweni Dam, Natal, in 1958; while the more detailed observations and paintings were made from this living material by the first writer in Port Elizabeth, Cape Province.

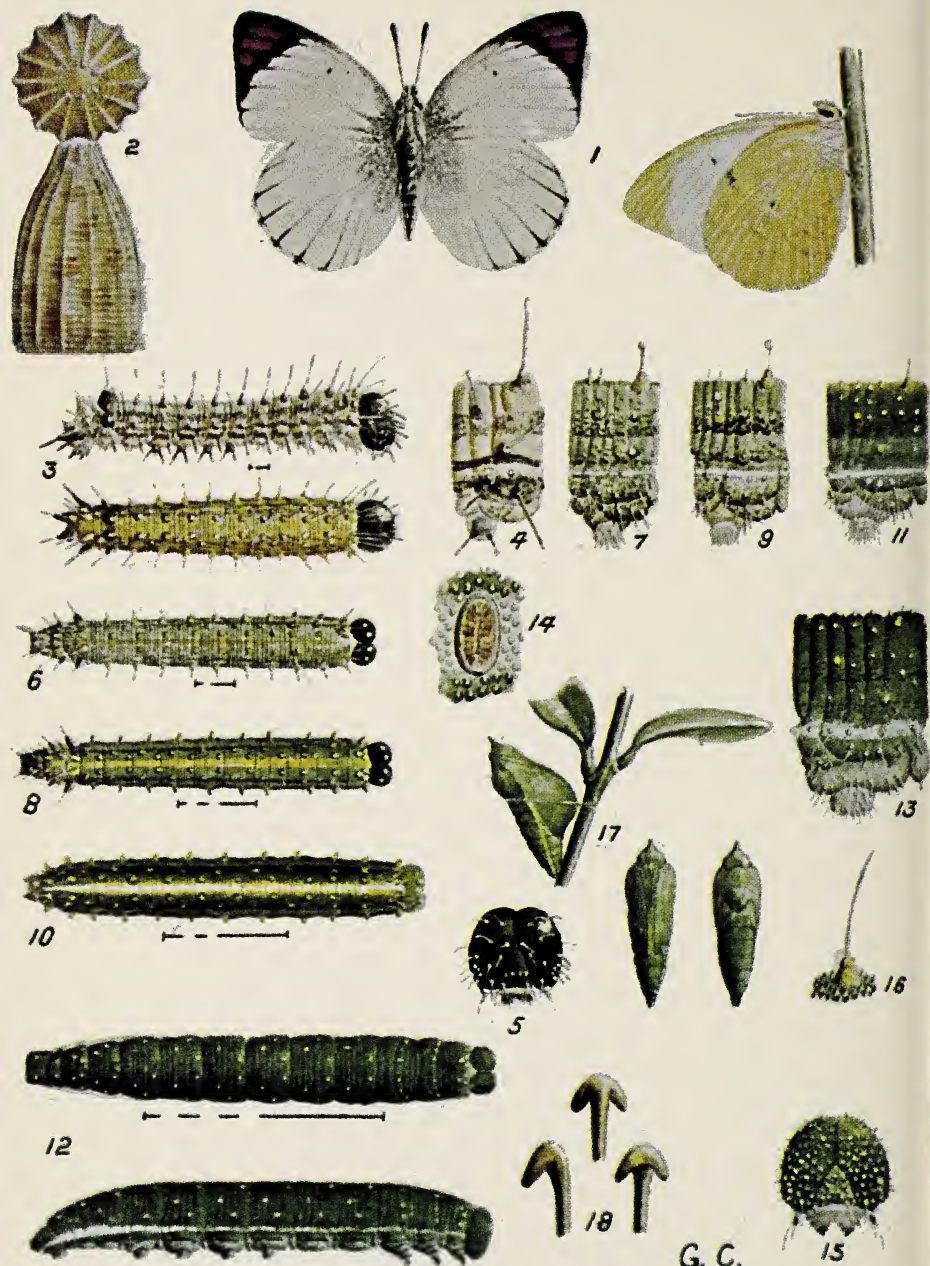
Colotis erone (Angus)

Egg. Eggs are laid singly, generally on a young shoot. They are pale yellow, darkening slightly in time and developing salmon spots, 0.6 mm. in diameter by 0.9 mm. in height and with 14-15 longitudinal ribs, only half of which reach the micropile. These ribs are cross-braced by some 25-28 lesser ribs. Eggs hatch after 4-7 days.

Larva. The larva eats its way out of the top of the egg and devours the discarded shell. It is 1.75 mm. in length on hatching and of a pale yellow colour, and soon develops brown longitudinal stripes. It feeds on the surface of a leaf and grows to 3 mm. in 6-12 days.

In the second instar larvae are pale green with brown mottled stripes and with the ventral parts dirty yellow. They grow to 5.5 mm. in 4 days.

¹C. G. C. Dickson, "Blencathra," Cambridge Avenue, St. Michael's Estate, Cape Town, South Africa.



COLOTIS ERONE (ANGUS)

for legend see page 41
GOWAN C. CLARK, del. ad. nat.

In the third instar larvae are of a darker green with firmer brown stripes and with the ventral portions yellow. They grow to 9 mm. in 3-4 days.

In the fourth instar larvae are of a still deeper green and the stripes are of a faint greenish-brown colour, the thin spiracular one of the two former instars still being present. There is a broad white dorsal line (which shows faint development in the previous instar). Larvae grow to 14 mm. in 4-5 days.

In the final instar larvae are green throughout with a thin white spiracular line. They feed on the edge of a leaf, filling the eaten-out gap with their bodies. They grow to 31 mm. in 7 days.

Pupa. The pupa is some 22 mm. in length and is mainly of green shades, to match its surroundings. It is secured in an upright position by cremastral hooks and a girdle. Emergence takes place after some 18 days.

A succession of broods occurs throughout the year, with a distinct seasonal difference both in markings and size.

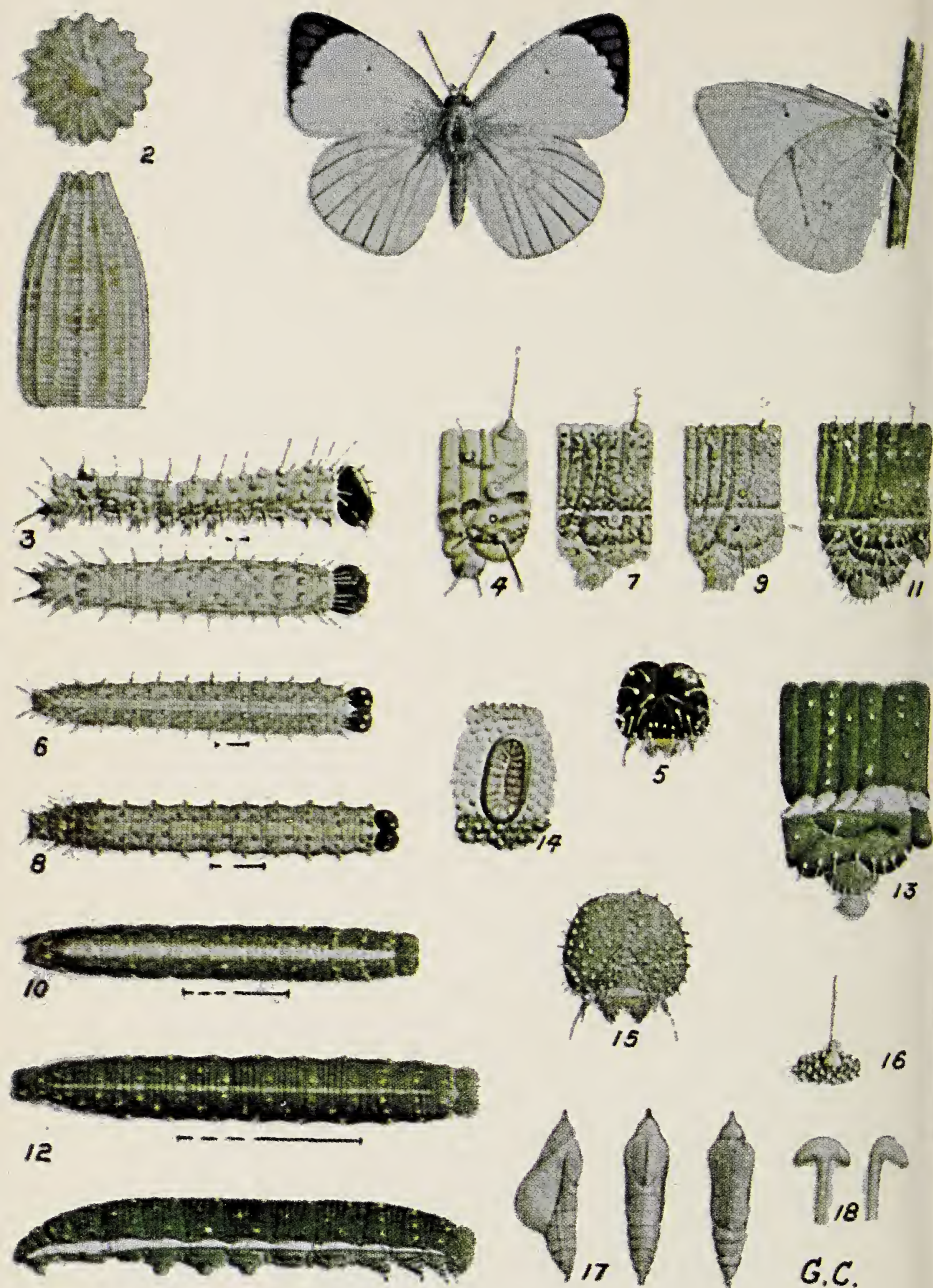
This butterfly has a quick, direct flight only a little distance above the ground, which has been rather aptly described as "jet-propelled" — in contrast to that of so many other Pierids. It is found in the open spaces in the neighborhood of the sub-tropical coastal forests or in glades and clearings in these forests, but it is also known to occur a short distance from the coast (of Natal) in places showing some approach to savannah country (e.g., at Shongweni Dam) and which, on the whole, are more characteristic as habitats of the following species, *C. ione*.

Food-plant : *Maerua racemulosa* (D.C.) Gilg. and Benn. (Capparidaceae) — *alternatiae* generic name: *Niebuhi*, as recorded originally by Platt (1921) for *Colotis erone*, i.e., *N. pedunculosa* Hochst.

Distribution. The only reliable records for this species appear to be those from or close to the coast of Natal and Pondoland — with a possibly dubious record from Swaziland. Most experienced workers, such as Mr. K. M. Pennington and Dr. van Son, do not now accept the earlier supposed locality records from other territories in Southern Africa, which may have resulted from confusion with *C. ione*.

***Colotis ione* (Godart)**

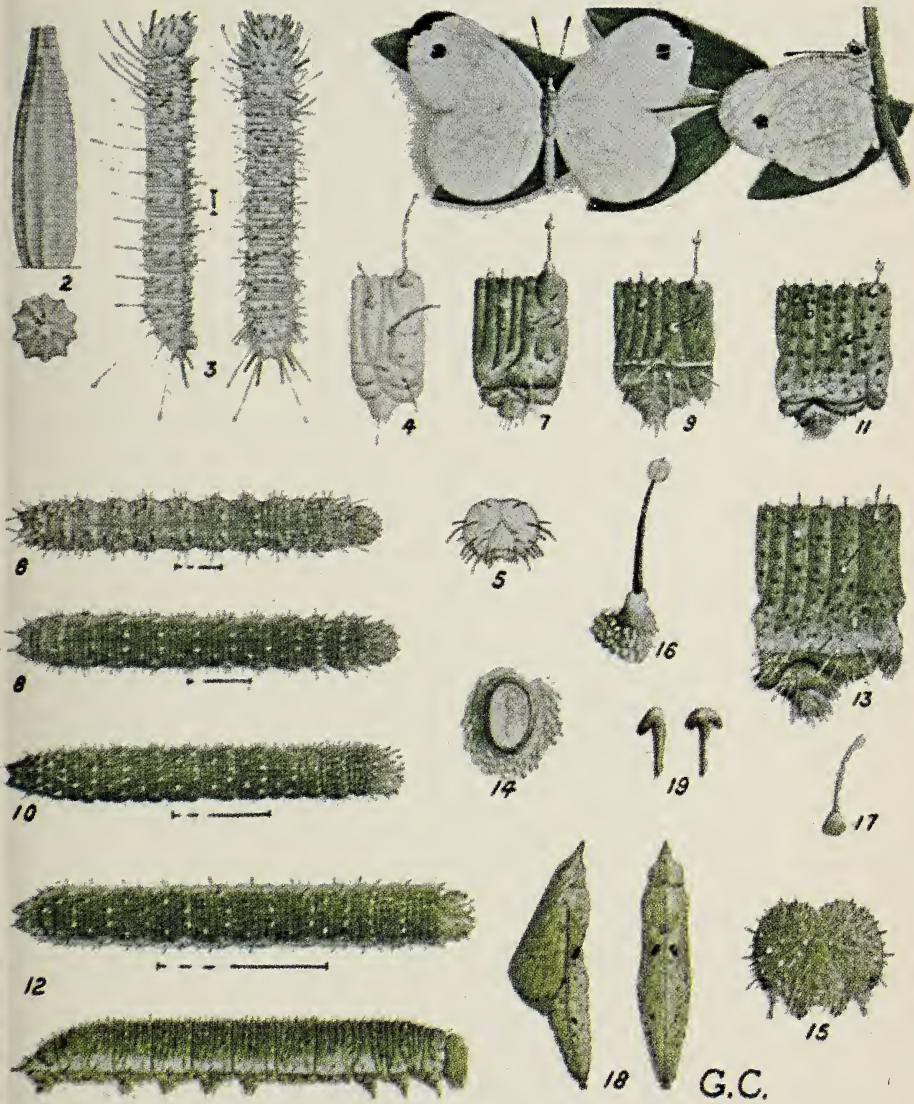
Egg. Eggs are laid singly on a leaf and are white at first but later assume a pale salmon tint with salmon spots. They are 0.45 mm. in diameter and 0.8 mm. in height and have 14-15



COLOTIS IONE (GODART)

for legend see page 41

GOWAN C. CLARK, *del. ad. nat.*



LEPTOSIA ALCESTA (STOLL.)
for legend see page 41
GOWAN C. CLARK, del. ad. nat.

longitudinal ribs, only 7-8 of which reach the micropile. The ribs are cross-braced by some 24 finer ribs. The larva emerges from the egg after 9 days.

Larva. The larva eats its way out near the top and the discarded shell is devoured. It is 1.25 mm. in length and of a pale yellow colour, later developing brown irregular lines in the vicinity of the spiracles. It feeds on a leaf's surface and grows to 2.75 mm. in 11 days.

In the second instar larvae are greyish with a whitish dorsal stripe. They grow to 4 mm. in 6 days.

In the third instar larvae are lighter grey, inclining to green, with a thin white spiracular line. They grow to 7 mm. in 6 days.

In the fourth instar larvae are green with white dorsal and pale green spiracular lines, while the anal segments are inclined to brown. They grow to 13.5 — 14 mm. (depending upon the sex) in 8 days.

In the final instar larvae are green with a thin pale-green dorsal stripe and a white spiracular stripe. The primary moles are yellow and very noticeable. Larvae grow to 23-24 mm. in 11 days. (The foregoing measurements applied to specimens which were below average size.)

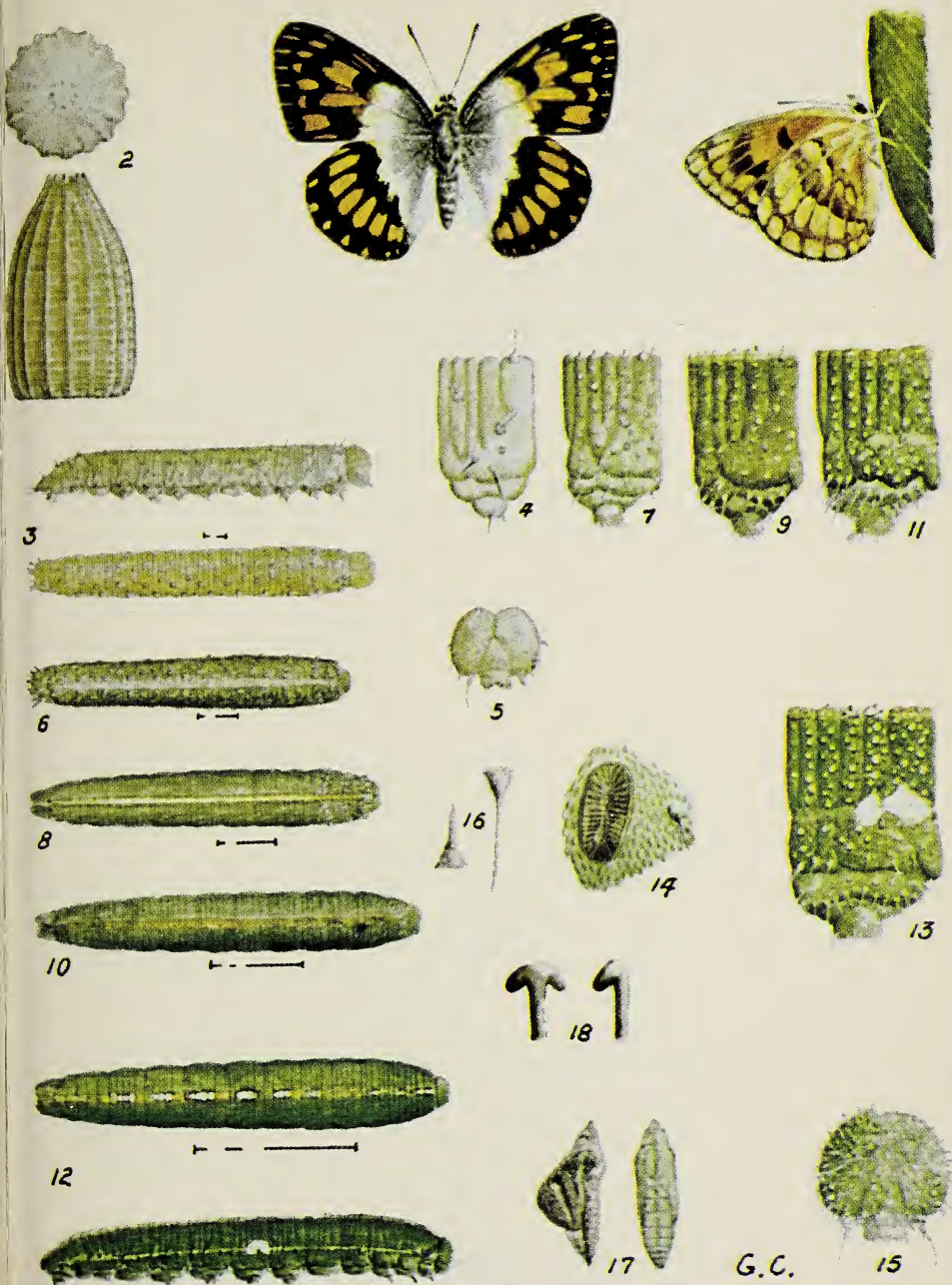
Pupa. The pupa is about 22 mm. in length and is whitish or green in colour. It is secured by cremastral hooks and a girdle, in an upright position. The butterfly emerges after some 18 days.

A succession of broods occurs throughout the year and, as in the previous species, there is noticeable seasonal difference in development of marking, colouring of the underside and size.

The flight is like that of *C. erone*. This species generally inhabits country of savannah types or areas transitional to it, but the butterfly occurs to some extent, anyway, on the Natal coast itself. In the writer's experience, it is decidedly scarce today, in comparison with *C. erone*, on the coast near Durban.

Food-plant : *Maerua racemulosa* (D.C.) Gilg. and Benn. (Cappiariaceae).

Distribution in Southern Africa. Pondoland (Port St. Johns — on the first writer's authority); Natal (from the coast to some distance inland in suitable areas) and portions of Zululand; S.W. Africa; Bechuanaland; N. and N.E. Transvaal; Rhodesia; Mozambique. Presumably, also Swaziland.



COLOTIS VESTA (REICHE)

for legend see page 41
GOWAN C. CLARK, *del. ad. nat.*

THE COMPLETE LIFE-CYCLES of the two species remaining do not appear to have been recorded previously or figures given of all the immature stages and these are therefore now being published, with all the stages represented in colour.

Material for these studies was procured in Natal: that for *Leptosia alcesta* on the coast, at Umhlanga Rocks, by the second author in 1955, and for *Colotis vesta* at Keat's Hill, on the Greytown-Dundee road, by Mr. T. W. Schofield, of Pietermaritzburg, in 1958, while the actual breeding and recording were done at Port Elizabeth, Cape Province.

***Leptosia alcesta* (Stoll.)**

Egg. Eggs are laid singly on young shoots. They are pure white, 1.5 mm. high by 0.4 mm. in diameter and have 10 longitudinal ribs, only 6 of which reach the micropile. These ribs are cross-braced by 28-30 fine ribs. Eggs hatch after 4-6 days.

Larva. The emerging larva eats its way out of the top of the egg and devours the discarded shell. It is 1.5 mm. long and is transparent water-white, the transparency, until it feeds on the leaves, making it difficult to see. It feeds on the edge of a leaf and grows to 3 mm. before moulting, after 6 days.

In the second instar larvae are greenish above and whitish below. They keep to one resting place, though they are not gregarious, and crawl away from it to feed. They grow to 6 mm. in 3 days.

In the third instar larvae are green throughout; they have the same habits as before and grow to 8 mm. in 3 days.

In the fourth instar larvae are of the same green colour but they have more setae. They grow to 12.5 mm. in 3 days.

In the final instar larvae are perhaps a shade darker in colour and there is a faint whitish sub-spiracular stripe. They grow to 22 mm. for male, and 23 mm. for female specimens in 10 days before pupating.

Pupa. The pupa is 15.5-16 mm. in length and is pale green. It is secured to a twig by cremastral hooks and is supported by a girdle. Emergence occurs after 10 days.

There is a succession of broods throughout the year, at any rate in the warm coastal portions of its range.

This delicate species has a very feeble flight and habitually

frequents the tropical or sub-tropical forests and their undergrowth, or at least localities in which the vegetation is sufficient to provide the shade in which it is usually found flitting about in its leisurely and rather restless manner.

Food-plant *Capparis zeyheri* Turcz. (Capparideae).

Distribution in South Africa. Natal (the coastal, or more coastal, zone); N. E. Transvaal; portions of Rhodesia; Swaziland; Mozambique.

***Colotis vesta* (Reiche).**

Egg. Eggs are laid singly on a leaf. They are white when laid but change to a pale yellow, are 0.45 mm. in diameter by 0.75 m.m. in height and there are 16 longitudinal ribs, only 9 of which reach the micropile. The ribs are cross-braced by some 24 small, fine ribs. Some eggs are faintly blotched with pale salmon. Eggs hatch 4 days after being laid.

Larva. The larva, on emergence, is 1.5 mm. long and is pale yellow throughout. It feeds on the younger leaves and grows to 3 mm. in 3-4 days.

In the second instar larvae are pale green with a light dorsal stripe. They grow to 5 mm. in 3 days.

In the third instar larvae are green with a yellow-bordered, whitish dorsal stripe. They feed on the edge of a leaf, occupying the part eaten out, with the dorsal stripe matching the missing edge. Larvae grow to 8 mm. in 3 days.

In the fourth instar larvae are green with a solid yellow dorsal line and a faint, whitish-green spiracular line has developed in this instar. They grow to 12-13 mm. in 3 days.

In the final instar larvae are green, with the dorsal line broken into alternate white and yellow portions, and each white portion thinly edged with brown. The spiracular line has widened into a white patch round the spiracle on segment VII. Larvae will now devour a whole leaf. They grow to 20-23 mm. in 4-5 days.

Pupa. The pupa is some 13.5 mm. in length and there is individual variation in colour from light green to shades of light brown. There is a well defined lateral stripe and the extended wing-case has a diagonal stripe. The pupa is secured by cremastral hooks and a girdle. The butterfly emerges after 6-11 days.

The broods are continuous throughout the year, with seasonal variation noticable in specimens.

This species is characteristic of certain tracts of country of more or less savannah type with a prevalence of native *Acacia* trees, sometimes interspersed with scattered but not very high bush. The flight is not as rapid as that of some of the other members of its genus.

Food-plant: at least one species of Capparideae.

Distribution in Southern Africa. Natal (excluding, from available records, the southern portion); S.W. Africa; Bechuanaland; N. and N.E. Transvaal; Rhodesia; Mozambique. Presumably, also Swaziland.

Much information pertaining to the two foregoing species, as regards the imagines, may be obtained from the works listed below.

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LEGEND TO THE FIGURES

COLOTIS ERONE

1. Imago, natural size
2. Egg — x 27
3. Larva on hatching
4. 7th Segment, 1st instar — x 60
5. Head, 1st instar — x 30
6. Larva, 2nd instar
7. 7th Segment, 2nd instar — x 30
8. Larva, 3rd instar
9. 7th Segment, 3rd instar — x 18
10. Larva, 4th instar
11. 7th Segment, 4th instar — x 10
12. Larva, final instar
13. 7th Segment, final instar — x 5
14. Spiracle enlarged
15. Head, final instar — x 5
16. Seta, much enlarged
17. Pupa, natural size
18. Cremastral hooks, much enlarged

COLOTIS IONE

1. Imago natural size
2. Egg — x 35
3. Larva on hatching
4. 7th Segment, 1st instar — x 65
5. Head, 1st instar — x 35
6. Larva, 2nd instar
7. 7th Segment, 2nd instar — x 60
8. Larva, 3rd instar
9. 7th Segment, 3rd instar — x 25
10. Larva, 4th instar
11. 7th Segment, 4th instar — x 15
12. Larva, final instar
13. 7th Segment, final instar — x 10
14. Spiracle, enlarged
15. Head, final instar — x 8
16. Seta, enlarged
17. Pupa, natural size
18. Cremastral hook, much enlarged

LEPTOSIA ALCESTA

1. Imago, natural size
2. Egg — x 20
3. Larva on hatching — x 30
4. 7th Segment, 1st instar — x 50
5. Head, 1st instar
6. Larva, 2nd instar
7. 7th Segment, 2nd instar — x 25
8. Larva, 3rd instar
9. 7th Segment, 3rd instar — x 16
10. Larva, 4th instar
11. 7th Segment, 4th instar — x 12
12. Larva, final instar
13. 7th Segment, final instar — x 9
14. Spiracle, enlarged

15. Head, final instar
16. Seta, enlarged
17. ditto
18. Pupa — x 2
19. Cremastral hooks, much enlarged

COLOTIS VESTA

1. Imago, natural size
2. Egg — x 16
3. Larva on hatching — x 30
4. 7th Segment, 1st instar — x 60
5. Head, 1st instar — x 25
6. Larva, 2nd instar
7. 7th Segment, 2nd instar — x 30
8. Larva, 3rd instar
9. 7th Segment, 3rd instar — x 20
10. Larva, 4th instar
11. 7th Segment, 4th instar — x 15
12. Larva, final instar
13. 7th Segment, final instar — x 10
14. Spiracle, enlarged
15. Head, final instar — x 9
16. Setae, enlarged
17. Pupa, natural size
18. Cremastral hooks, much enlarged

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A NEW SPECIES OF *FERALIA*

FROM SANTA CATALINA ISLAND OF CALIFORNIA, WITH NOTES
ON THE IMMATURE STAGES OF *FERALIA FEBRUALIS* GROTE
(NOCTUIDAE:CUCULLIINAE)

JOHN S. BUCKETT

University of California
Davis, California

WHILE IN THE UNITED STATES NATIONAL MUSEUM, Washington, D. C., in January, 1964, it was the author's pleasure to discover an apparently new species, or subspecies of *Feralia* that was closely allied to *februalis* Grote. Upon further studies, in particular genitalia mounts, it was found that *meadowsi* Buckett, new species was distinct anatomically as well as by maculation from *februalis*. The specimens of this new species were all collected during the short interval between 1930 through 1933 by the amateur Lepidopterist, Schoolteacher, Mr. Don C. Meadows.

The Los Angeles Times Sunday Magazine for 26 February 1933, pg. 16, states, "For five years Master of Science Don C. Meadows, moth-man of Catalina Island, has been studying 'fly-by-nights,' and he has captured 400 different species of moths, many of which are newer to entomology than the neutron is to physics." Even though the specimens are labeled "Avalon," the article further states "Prof. Meadows sets the trap in canyons back of Avalon . . ." This statements leads one to infer that it is quite possible that *meadowsi* may have been collected in mountainous canyons of the island.

Judging by its affinity to *februalis*, one wouldn't expect *meadowsi* to be an unusually rare moth during the early part of the year. Its scarcity in collections is probably due to the lack of collecting on the Channel Islands. *F. februalis* is not a species which flies great distances, and most ilikely *meadowsi* would exhibit a similar habit. Santa Catalina is over 20 miles from the mainland, and it is highly unlikely that *februalis* and *meadowsi* have come in contact with one another for sometime by natural means, yet the two species are obviously closely related. I take great pleasure in naming this species after the ardent "moth-man of Catalina Island," Mr. Don C. Meadows.



Fig. 1. Holotype male, *Feralia meadowsi* J. S. Buckett. Avalon Club House, Santa Catalina Island, California, 23 February 1933 (D. C. Meadows).

Fig. 2. Allotype female, *F. meadowsi*. Same locality and collector as holotype, 10 February 1932, Bauer-Buckett slide No. 67D17-53 (in U.S.N.M.).

***Feralia meadowsi* J. S. Buckett, new species**

Male: Ground color of primaries dorsally pale green (Specimen compared to Reinhold Color Atlas, pl. 27 A3); secondaries dorsally with black dots at anal angle. Head with vertex clothed in whitish and pale green dentate scales and hairs; frons clothed dorsally in short black simple scales, medially clothed as in



Fig. 3. *Feralia februalis* Grote, male. Santa Rosa, Sonoma County, California, 14 December 1954 (J. S. Buckett). This is the typical *februalis* which expresses very little transverse blackish coloration of the primaries.

Fig. 4. *F. februalis*, male, illustrating slight transverse blackish coloration. Inverness, Marin County, California, 31 January 1964 (J. S. Buckett & M. R. Gardner).

vertex, cuticula externally with minute reticulations, otherwise smoothly rounded; maxillary palpi exterolaterally black, ventrally clothed in whitish and brown flattened hairs, terminal segment greatly reduced; antennae bipectinate, each bipectination bearing ventrally directed ciliations, becoming setose apically; compound eyes moderately lashed with elongate brownish hairs.



Fig. 5. *F. februalis*, male, illustrating an extreme amount of transverse blackish coloration. Middletown, Lake County, California, 12 February 1955 (W. R. Bauer & J. S. Buckett).

Fig. 6. *F. februalis*, female, illustrating extreme transverse blackish coloration, as well as an olive ground color of primaries. Cobb Mountain, Lake County, California, 7 March 1959 (W. R. Bauer & J. S. Buckett).

Thorax dorsally with divided collar basally, with weak black dash, medially pale green, apically white tipped; tegulae with anterior-most portion clothed in jet-black dentate scales; inner, posterior and exterior margins of tegulae bound subterminally in black, terminally white; disc clothed in pale green, white and black dentate scales; ventrally clothed in blackish simple hairs

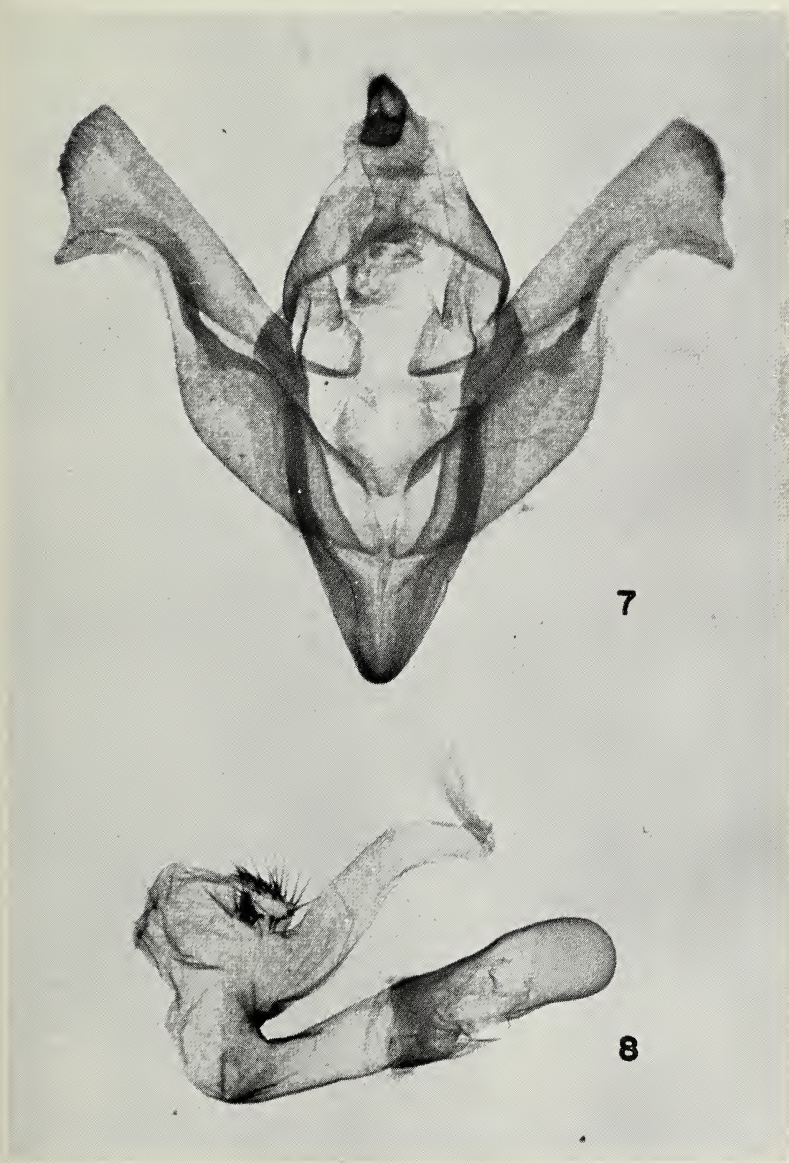


Fig. 7. *F. meadowsi*, male genitalia minus aedeagus. Avalon, Santa Catalina Island, California, 12 November 1931 (D. C. Meadows), Bauer-Buckett slide No. 67C31-21 (in U.S.N.M.).

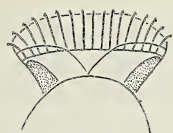
Fig. 8. *F. meadowsi*, aedeagus. Data same as for fig. 7.



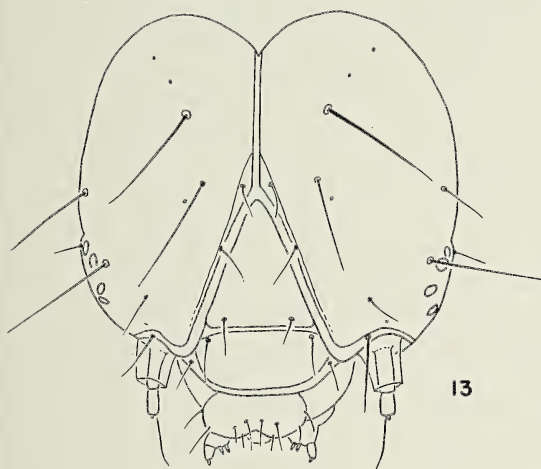
Fig. 9. *F. februalis*, male genitalia minus aedeagus. Inverness, Marin County, California, 31 January 1964 (J. S. Buckett & M. R. Gardner), Bauer-Buckett slide No. 67C31-23.

Fig. 10. *F. februalis*, aedeagus. Data same as for fig. 9.

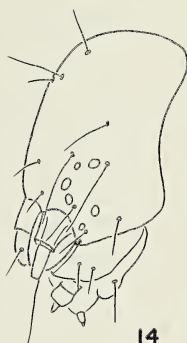
anteriorly, remainder clothed in white simple hairs; legs with femora clothed dorsally in blackish scales, ventrally clothed in elongate whitish hairs; tibiae and tarsi banded, black and white; primaries dorsally with ground color pale green; basal line geminate, terminally white; basal and transverse anterior areas of ground color; transverse anterior line represented costally as



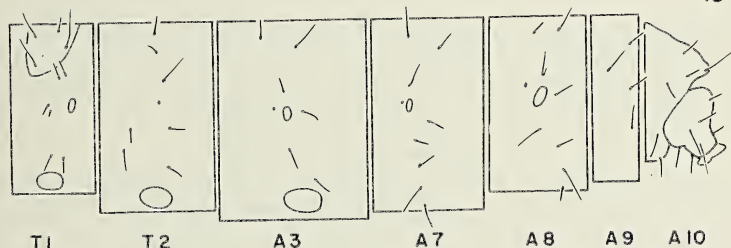
12



13



14



15

Figs. 11-15, *Feralia februalis*.

Fig. 11. Mesal view of proleg, fifth instar larva, illustrating crochets.

Fig. 12. Mesal view of right mandible, fifth instar larva.

Fig. 13. Frontal view of head, fifth instar larva.

Fig. 14. Lateral view of head, fifth instar larva.

Fig. 15. Setal maps showing chaetotaxy of fifth instar larva, lateral view.

T1, T2 = Thoracic segments 1 and 2, respectively; A3, A7, A8, A9, A10 = Abdominal segments 3, 7, 8, 9, 10 respectively.

black wedge, weak from subcosta to cubitus, thence geminate, basally black, apically whitish; median area of ground color for most part, orbicular squared off, weakly outlined in black, thence white, centrally of ground color; median line irregular, black; reniform an open "figure 8," colored as in orbicular; transverse

posterior line very jagged, geminate, basally white, apically black, commencing on costa just basally of subterminal line, thence meandering onto lower portion of reniform, thence proceeding to inner margin where it intersects closer to tornus than to median line; tornus area with conspicuous black dash; subterminal line a black wedge on costa, thence diminishing and fading out in the vicinity of M_1 ; combined subterminal and terminal areas washed with whitish, therefore appearing very pale, or "washed out;" terminal line represented as black undulating line, dipping basally between veins, fringes checkered, black and pale green; ventral surface whitish, with slight trace of pale green; basal, transverse anterior, median, and subterminal lines represented costally in black, thence wanting; veins faintly outlined in brownish; terminal line and fringes as in dorsal surface, but paler; secondaries dorsally whitish, with slight suggestion of black exterior line; inner margin clothed in tan elongate hairs; terminal line as in primaries; fringes pale green; ventral surface possessing two faint transverse black lines; fringes as in dorsal surface. Abdomen dorsally clothed in brownish and tannish hairs, for most part, some very stout; terminally clothed in whitish and blackish simple and flattened hairs; laterally clothed in blackish hairs and scales; ventrally clothed in whitish simple hairs. Greatest expanse of forewing 16 mm. Genitalia as in figures 7 and 8.

Female: As in male, except antennae weakly fasciculate instead of being bipectinate. Judging by the single female at hand, this sex seems to be of lesser forewing expanse than in the male (this is not necessarily the case in *februalis*, though).

Specimens examined

Holotype male, Avalon Club House, Santa Catalina Island, California, 23 February 1933 (Don C. Meadows), U.S.N.M. type no 64645. Paratypes: 1 female, 13 males; 1 female (designated Allotype), same locality and collector as holotype, 10 February 1932; 13 males, same locality and collector as holotype, 12 November through 19 February, 1930-1933; all in United States National Museum except for a single male dated 8 January 1932, in Bauer-Buckett Collection, Davis, California.

Judging by the series of 15 specimens before me, the Santa Catalina Island species is more constant in color and in maculation than the mainland species, *februalis*, its closest relative. *F. meadowsi* differs from *F. februalis* superficially by its constant, drab, pale green coloration; pronounced black lunule, or dash of the tornus area on dorsal surface of primaries; constant

conspicuous black spot at anal angle of secondaries, dorsally.

The male genitalia of *meadowsi* are distinctly different from *februalis* in that *meadowsi* possesses a broader cucullus, much broader valvae, and broader ventral process of the terminal portion of the uncus. The aedeagus possesses considerably fewer spines on the vesical sac also. The female genitalia of *meadowsi* differ from *februalis* by the former possessing virtually no large setae on the ovipositor lobes, whereas *februalis* possesses many; *meadowsi* has a less sclerotized ductus bursae, and the genitalia on the whole is of lesser size than is *februalis*. The single female before me probably is representative of *meadowsi*, but it could be a teneral individual.

The immature stages of *Feralia februalis* have been briefly discussed (at least the fifth instar) by Crumb (1956); however, to my knowledge, the chaetotaxy of the fifth instar larva has not been described or illustrated. Crumb (op. cit.) states in his key to known species of *Feralia* larvae that *februalis* "Feeds on broad-leaved trees." Under the description of *februalis* he cites as food plant "*Cercocarpus betuloides* and oak (*Quercus douglasii*).". The author has been successful in rearing this species on California Buckeye, *Aesculus californicus* (Spach) Nuttall, from eggs obtained from an adult female, and McFarland (Master's Thesis) cites *Sambucus*, *Cercocarpus* and *Quercus* as host plants for *februalis* in southern California.

Crumb described the general habitus of the fifth instar larva and therefore it will not be necessary to do so here. In the key as well as in the description, he stresses the presence of a "very decided subconical dorsal hump on 8." The eighth abdominal segment on my three preserved fifth instar larvae lacks this "subconical hump;" however, on a second instar larva there is a suggestion of this hump. Chaetotaxy of the pertinent thoracic and abdominal segments may be seen in fig. 15. Chaetotaxy of the head may be seen in both front and lateral views (as in figs. 13 and 14, respectively).

At this time, I would like to express my appreciation to Mr. Michael R. Gardner for preparing the illustrations of the larva of *februalis*. The genitalia slides were made using lignin pink stain and balsam as the mounting media.

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HOMONYMY
OF THE "NEW GENUS" *PETALUMA* BUCKETT AND BAUER
(NOCTUIDAE) UNDER *PETALUMA* HULST (PYRALIDAE) AND
PROPOSAL OF THE NAME *PETALUMARIA*
FOR "*PETALUMA*" CALIFORNICA.

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IN 1964 (J. Res. Lepidoptera) the authors named a new noctuid moth *Petaluma californica*, new genus and species, the generic name being preoccupied. The name *Petaluma* Bkt. and Br. is then a primary homonym of *Petaluma* Hulst. This error stemmed from not having referred to "Nomenclator Zoologicus" by Neave. Only recently the first author was checking "Nomenclator Zoologicus" in connection with another new generic name to be proposed in a manuscript in preparation, and while doing this, he thumbed into the "P" section and looked to see if *Petaluma* was listed. There, appearing in bold print, was "*Petaluma* Hulst 1888, Ent. Amer., 4, 116 — Lep." The irony of the situation is worthy of note, as the name was used in the Lepidoptera, Phycitidae.

Petaluma illibella Hulst, the type species of the genus is now placed under the genus *Coenochroa*, in the subfamily Anerastiinae of the Pyralidae.

We herein propose *Petalumaria*, new generic term, for the species "*Petaluma*" *californica* Bkt. and Br. The type species of *Petalumaria* is *P. californica* (Bkt. and Br.).

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REARING EULEUCOPHAEUS RUBRIDORSA AND E. LEX (SATURNIIDAE)

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INTRODUCTION

FINAL AND PENULTIMATE INSTAR LARVAE of *Euleucophaeus rubridorsa* Felder and *E. lex* Druce were collected in the vicinity of the Great Pyramid, Teotihuacan, near Mexico City about the middle of September 1961 by Dr. A. D. Blest and Dr. T. S. Collett who kept them in plastic boxes and delivered them to me in England on 26. IX. 61. Upon receipt the larvae, which were as yet unidentified, were sorted into two species and reared separately.

When the larvae arrived both were feeding on rather dried leaves of some species of Leguminosae which it was not possible to identify, but from the leaf form and bits of stem appeared to be a kind of prickly Mimosa. This was the plant from which the wild larvae had been collected. They were offered various European trees and shrubs and the rearing was carried out at 20-25°C. under natural conditions of British daylight.

EULEUCOPHAEUS LEX

On receipt the larvae were offered *Robinia pseudo-acacia* to which they transferred after a few days. As the leaves of this tree shortly began to fall *Fagus sylvatica* was later offered and this too was accepted by all the larvae.

The larvae were very slow in their movements and showed no sign of being gregarious. When disturbed there was a tendency for them to drop and curl up on the ground although this reaction is by no means so intense as I have observed in, for instance, *Automeris vinosus* Conte, and is about equal to the intensity in the final instar larvae of the rather better known *Hemileuca maia* Druce.

About 80 larvae were received. Of these 25 per cent died for unknown reasons and a further 25 per cent produced parasites of the genus *Apanteles*. It has not to date been possible to determine the exact species). From 12-24 specimens of *Apanteles* emerged through the skin of each *lex* larva. They then proceeded to spin their oval white cocoons amongst the spines of the larva. The adult parasites emerged about a week after pupation. It is interesting to speculate what they then do in nature. The first adult parasites appeared only 16 days after receipt of the larvae and there seems no doubt that they would be emerging simultaneously in Mexico. What then does the next generation live on? The *lex* larvae are now all final instar. Do the *Apanteles* (which normally parasites the early instars of Lepidopterous larvae) have an alternative host? Here is an opportunity for some field research in Mexico.

Even more curious is the failure of the *Apanteles* to kill the *lex* larvae immediately. Although a few remained motionless after the parasites had emerged, most of them continued to walk slowly about, without feeding, for up to 14 days before dying. The adult parasites were thus emerging before the death of their host.

The remaining 50 per cent of the larvae successfully pupated. Pupation took place in a flimsy cocoon, generally in the corners of the rearing cage, a few amongst the leaves of the foodplant, where it would probably normally occur in nature. The pupa itself is a bluish-black color and it and the cocoon case is covered with a white powder. A similar powder occurs in certain Lasio-campidae but in no other Saturniid genus known to me.

The full-grown larva is cylindrical, about 4-4.5 cms. long. Head black. Dorsally velvety-black, densely covered with reddish-brown and golden-yellow slightly raised minute dots many of which bear a short white hair. The colors of these dots are so arranged as to give the effect of a yellowish lateral line, above which is orange, then yellow again and finally an orange dorsal line. The chalazae are short, black, bearing dense spines which are black at the base with white tips. Spiracles inconspicuous. Ventrally, the ground color black, covered in grey slightly raised spots each bearing a whitish hair. Legs similarly marked.

The duration of the final instar was 34 days and of the pupal stage (based on 4 individuals only — the rest of the pupae having been used for other purposes) — 60 days. The moths were noted to be diurnal flyers.

EULEUCOPHAEUS RUBRIDORSA

On receipt the larvae were offered *F. sylvatica* which was at once accepted. *R. pseudo-acacia* was also found to be eaten.

The final instar larvae are rather more active than those of *lex*, show the same tendency to drop when disturbed and also spin a flimsy cocoon in the corners of their cage or among the leaves of their foodplant. Similar in color and appearance; also covered with whitish powder.

Only a few of the larvae died and although none produced any *Apanteles* parasites, three of them produced a dipterous parasite each. These were a single female *Spoggosia* (*Spoggosia*) *floridensis* (Tns.) and two male *Leschenaultia* sp. near *leuco-phrys* (Wied.) and *fusca* Tns. These are the first records of Tachinidae from this host.

The full-grown larva is cylindrical, about 4.45 cms. long. Head black with fine, sparse, whitish hair. Ground color dark grey, covered in lighter grey or silver round and oblong slightly raised, very small and numerous spots which, laterally and ventrally bear whitish hairs. These are so clustered as to form a distinct lateral lightish silver-grey line. The chalazae very short and with very dense spines, these being whitish-grey at base with black tips. The legs black with whitish-grey spots and whitish hairs.

As with *lex*, most of the pupae were used for other purposes and only a few moths emerged. The first female to do so did not expand her wings until 18 hours after eclosion. This is the only instance known to me of such a long delay, It being my experience that unless wing expansion occurs within minutes of eclosion then it does not take place at all. This case was obviously exceptional and no other instance of it occurred either with this species, with *lex*, or amongst the many specimens of the closely related *Hemileuca* spp. that I have bred.

The moths are diurnal, and shortly after this female had expanded her wings she commenced to "call" and was paired in the afternoon in bright winter sunlight. Copulation lasted between 30 and 45 minutes. She commenced to oviposit just after dusk and laid 158 ova in two batches. She was very active the following day but died that night without laying any more. She was found to be empty of ova. Another virgin that was dissected was found to contain 155 ova. The ova are large for the size of the moth. When first laid they are jet black, but within 1-2 minutes fade to the brown color of milk chocolate, with a black micropyle. They were laid in a regular mass on the side of the

cage containing the female. In nature probably in a ring round twigs like *H. maia* does. The eggs were kept at $15^{\circ}\text{C.} \pm 5^{\circ}\text{C.}$ and hatched in 59 days.

The newly hatched larvae were transferred to 25°C. and offered a choice of *Salix* sp. (which had been forced in a heated greenhouse) and various Graminae. After 48 hours they commenced to feed on the *Salix*, but two days later they at once transferred to *Mimosa dealbata* when this was offered them. At this stage, and for the next few instars, they are strongly gregarious and move in single file columns. When feeding they form a tight cluster and feed gradually outwards from the base of the leaves towards the tip. When they reached the fifth instar the *M. dealbata* gave out and *Quercus ilex* was offered and accepted. Unfortunately after the 7th moult the majority of the larvae died of what appears to have been a granulosis virus disease, although absolute confirmation of this has not yet been possible.

The fact that this disease occurred in a subsequent generation, and at such a great distance from any natural specific source, is strong evidence that this was a trans-ovarially transmitted disease.

The duration of the various stages can be summarized as follows:—

Egg stage at $15^{\circ}\text{C.} \pm 5^{\circ}\text{C.}$	= 59 days
1st instar larva at 25°C.	= 10 "
2nd " " " $20^{\circ}-25^{\circ}\text{C.}$	= 11 "
3rd " " " "	= 7 "
4th " " " "	= 12 "
5th " " " "	= 18 "
6th " " " "	= 11 "
7th " " " "	= 15 "
8th " " " "	= 30 "
Pupal stage " "	= 42 "

which gives a total of 215 days or seven months.

DISCUSSION

It has been possible to rear one species, *rubridorsa*, right through from egg to adult for the first time. The complete life-cycle period of seven months is an odd one and unlikely to be found in nature where the species is either double-brooded with a six-month cycle, or, perhaps rather more likely, at some stage or other diapauses, probably in the egg stage like *H. maia*. My eggs were kept comparatively warm at $15^{\circ}\text{C.} \pm 5^{\circ}$ and I have known

maia eggs, when also kept warm hatch within two months instead of overwintering.

The number of larval instars is eight, which is high for a Saturniid, many species of which have but 5 or 6 instars. Combined with this is the very long larval period of 114 days, which is nearly double that of *Hylesia nigricans* Berg, the only other Saturniid I am acquainted with which also has eight instars, and which when reared under comparable conditions, has a larval period of 64 days. The very slow and lethargic movements, combined with several days spent in moulting, supports the belief that this figure is a true one, probably corresponds to that found in Mexico, and is not attributable to the unfamiliar food that was being eaten.

With the other species, *lex*, it was not possible to determine the complete life-cycle. Nevertheless, some useful information was obtained, the duration of the final instar and pupal stages being determined and also that this is a diurnal moth. In Mexico there seems little doubt that the two species are nearly contemporaneous.

Like all Hemileucine larvae the spines can give a painful sting when brushed against. The effect of both these species is similar, and not very painful, at any rate to the author!

Very little appears to be known about the early stages or life-histories of the genus *Euleucophaeus* and several inaccurate and vague statements have been made about it. According to Michener (1952) most of the species are Mexican with a few ranging north to Arizona and Kansas. A study of the distribution of the various species given by Draudt (1930) confirms this. Crotch (1956) states, incorrectly, that they are all South American.

Draudt (1930) also states that "all of them (the larvae) probably live on grass". Crotch (1956) that "the larvae are thought all to be grass-feeders". However, the only species that have actually been found feeding on grass are *mania* Druce and *oliviae* Cockerell (Draudt, 1930). Both *lex* and *rubridorsa* have to spin their oval white cocoons among the spines of the larva. now been found in the wild feeding on a tree or shrub which, although exact determination was not possible, was clearly of the family Leguminosae and the larvae were found subsequently to feed on other members of this family, *Robinia* and *Mimosa* as well as various Fagaceae. (It is my experience of Saturniids that all species perhaps normally found on Leguminosae in the tropics will accept temperate zone Fagaceae).

The dipterous parasites were too few to give any indication of specificity, but is perhaps significant that only *lex* had been parasitised by an *Apanteles* species, since the two species were occurring together at the same stage. Nevertheless, as already surmised, it seems that the *Apanteles* must have an alternative host.

ACKNOWLEDGEMENTS

I would like to thank Dr. R. W. Crosskey of the Commonwealth Institute of Entomology for naming the parasitic Diptera.

This work, including Dr. Blest's and Dr. Collett's expenses in the field, was supported by the United States Institute of Health (Project GM. 07109).

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NEW RECORDS, AND NOTES ON
THE STATUS OF SOME HESPERIIDAE FROM
MEXICO

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WHILE AT THE UNITED STATES National Museum in Washington, D. C. during July 1966 I had the opportunity of examining all of their American HesperIIDae and especially their specimens from Mexico. One particular reason for this trip was to check carefully their types and especially those of Dyar that W. H. Evans had placed in synonymy. The results were very interesting in that several of Dyar's "synonyms" were found to be valid species and I will make some remarks in this article pertaining to two of these. Others will be discussed in a later publication.

In the American Museum of Natural History, New York, are located most of E. L. Bell's types of tropical American HesperIIDae, however there is one in particular in Washington that has long interested me. This species is *Mellana mulleri* (Bell) from Mexico which Evans placed as a synonym of *eulogius* (Ploetz) in 1955. While Bell was active at the American Museum of Natural History we corresponded concerning the various species of *Mellana* (then *Atrytone*) that he had described and it surprised me to see that Evans had placed *mulleri* as a synonym of *eulogius* due to several reasons that I will discuss under that species.

Among specimens sent to me by Dr. Tarsicio Escalante, Mexico, D. F., for determination were found two species previously unrecorded for Mexico.

***Bolla cyclops* (Mabille) 1876**

During 1953 Evans described *sonda* as a new subspecies of

¹I would like to express my thanks to the National Science Foundation for Research Grant GB4122 which is making this study of the HesperIIDae of Mexico possible.

cyclops from Orizaba, Veracruz, Mexico, based on differences in the coloration of the lower surface of the primaries. Apparently he failed to check the genitalia as there are specific differences present between *sonda* and *cyclops*. For quick determination the coloration is sufficient as *sonda* is dusky ochreous on the lower surface of the primaries, whereas *cyclops* is a bright yellow.

Previous records indicate that *cyclops* had been collected from Guatemala to Colombia, while *sonda* was more or less confined to the section of Veracruz in Mexico near Orizaba.

Among specimens received from Dr. Escalante were five examples of *cyclops*, one male, and four females, all from Sta. Rosa, Comitan, Chiapas, Mexico (May 1965). This is the first record of *cyclops* from Mexico.

Piruna cyclosticta (Dyar) 1920

This species was placed as a synonym of *brunnea* (Scudder) 1872 by Evans in 1955. Since that time I have collected rather widely over Mexico and found that actually there are two species involved that somewhat resemble each other superficially. While in Washington I examined the type of *cyclosticta* and found that it agreed with some specimens that I had from Tehuacan, Puebla (August 14, 1964, H. A. Freeman) and Aguas Calientes, Aguascalientes (August 1956, Stallings & Turner), and also that the figure in Seitz of *cyclosticta* was very accurate. The information contained in Evans key to *brunnea* does not agree with *cyclosticta*. I have specimens of *brunnea* from Oaxaca, Oaxaca (June 23, 1966, H. A. Freeman), and Tierra Colorada and Acahuizotla, Guerrero (August and September). There are specific differences in the genitalia, however the easiest way to separate the two species is by the following differences: (1) *brunnea* is slightly larger, average total expanse, 26mm., whereas *cyclosticta* averages 22 mm.; (2) *brunnea* never has a second spot in space 2 located between the distal spot in that space and the base, while *cyclosticta* has such a spot present; (3) *brunnea* is darker than *cyclosticta* being nearly black, while *cyclosticta* is more grayish-brown; and (4) all spots are better defined in *cyclosticta* than they are in *brunnea*.

Apparently the only material examined by Evans was the four specimens from Oaxaca, Mexico and the one from Guatemala contained in the British Museum. These are all *brunnea* as all that I found in the Oaxaca area was that species. In the state of Puebla northwestward to Aguascalientes only *cyclosticta* was found.

From the above mentioned information I am removing *cyclosticta* from the synonymy of *brunnea* and giving it full specific status.

***Dalla dividuum* (Dyar) 1913**

This species was placed as a synonym of *ligilla* (Hewitson) 1877 by Evans in 1955. After carefully examining the type of *dividuum* (Dyar) in Washington I found that it matched perfectly the figure of that species in Seitz, and did not agree with his figure of *ligilla*. Recently I obtained a number of specimens of *ligilla* from Dr. Escalante that were collected at Catemaco, Veracruz, and Comitán and Ocozingo, Chiapas. These agreed perfectly with the figure in Seitz of that species as well as Evans' sketch of the male genitalia, so there is no doubt as to their status. During July 1967 I received from Robert Wind four males and a female *Dalla* that he had collected at Salada, Colima, Mexico during June 1967. These I mounted and noticed at once that they agreed with the figure in Seitz of *dividuum*, and also with the notes that I had taken of the type in Washington. I dissected a male and noticed that the genitalia were not like those of *ligilla* so proving beyond a doubt that actually there are two separate species involved. The figures of the genitalia of these two species will be presented in a later publication. There are several differences that are readily discernable between these two species: (1) *ligilla* is slightly larger averaging 30 mm. total expanse, while *dividuum* averages 28 mm.; (2) the elongated spot in space 3 of *ligilla* overlaps the spot in space 2 and reaches the outer edge of the cell spot, while in *dividuum* this spot is a tiny dot located beneath the apical spots and well separated from the spot in space 2 and the cell spot; (3) in *ligilla* the large yellowish central spot on the upper surface of the secondaries is not broken by dark veins, while in *dividuum* it appears macular due to the presence of dark veins; (4) on the lower surface of the secondaries *ligilla* has a dark brownish area between the discal spots and the margin which is not present in *dividuum*; and (5) on this same surface in *ligilla* there is one large yellowish spot located below the costa and situated over the large upper discal spot and the elongated cell spot, while in *dividuum* there are two smaller spots located in this same area.

From the information presented there is no doubt as to the specific validity of the name *dividuum* and with this I remove the name from the synonymy.

Mellana mulleri (Bell) 1942

E. L. Bell described *mulleri* in 1942 from four specimens that were collected in the state Guerrero in Mexico. The type is in the United States National Museum and I examined it while I was there. Evans recorded this species under the synonymy of *eulogius* (Ploetz) as “? *mulleri* Bell 1942: male Mexico: genitalia figured”. The question mark indicating that he was not certain about this as apparently he had not examined the type. *Eulogius* is a very variable species and I have collected it in a number of areas in Mexico as well as at Brownsville, Texas. It is very common in parts of Guerrero, Puebla, and especially in the Valles area of San Luis Potosi. I have in my collection over fifty specimens of that species and even though it is variable it does not ever show the distinguishing characteristics of *mulleri*. During August 1962 I collected two males and five females of *mulleri* in the mountains just west of Ciudad Victoria, Tamaulipas, Mexico. Both males were dissected and compared with Bell's drawing of the genitalia of *mulleri* and a number of the genitalia of *eulogius* so as to make a careful comparison between the two. It was a simple matter to readily separate the two species since *mulleri* has one of the most distinctive genitalia of the *Mellana*. Godman and Savin present a fine drawing of the genitalia of *eulogius* under the name of *mellona* Godman in their Biologia Centrali-Americana, plate 94, figure 19. Actually, in appearance, *mulleri* more closely fits in with the *nayana* Bell group than with the *eulogius* group but can be separated by the genitalia very easily. By superficial characteristics *mulleri* males differ from *eulogius* in the following ways: (1) in *mulleri*, on the upper surface of the primaries, the fulvous coloration is more extensive than in the most extreme examples of *eulogius* as represented by the figures of *mellona* plate 94, figures 17 and -8 in the Biologia; (2) in *mulleri*, on the upper surface of the secondaries, the discal fulvous spots are much broader than in *eulogius* thus producing a more narrow brown outer margin; (3) on this same surface, the easiest way to separate the two species is in the shape of the spots in spaces 5 and 6. In *eulogius* these spots are smaller than the rest of the discal band and the spot in space 5 does not touch the cell spot, while in *mulleri* the spot in space 5 is the largest in the discal band and touches the cell spot, and the spot in space 6 is elongated and situated directly over the center of the spot in space 5; and (4) *mulleri* has a somewhat blurred appearance due to the suffusion of

fulvous scales over the dark areas of the upper surface of the primaries. *Eulogius* does not have this appearance even in the lighter specimens where the fulvous coloration is more extensive than in the typical examples. In the females the differences can be determined by the following characteristics: (1) *mulleri* is a much browner species, with rather indistinct fulvous maculation on the primaries, while *eulogius* is dark with a slight olive cast, and the maculation is distinct with the spots in spaces 2 and 3 white; (2) *mulleri* has a double fulvous cell spot over the inner edge of the spot in space 2, while *eulogius* rarely has any spots in the cell area, if present they are situated inward from the spot in space 2; and (3) in *mulleri*, on the upper surface of the secondaries, the discal band is broad and rather indistinct, while in *eulogius* the discal band varies from none at all to a clearly defined row of yellow spots. *Mulleri* differs from *nayana* (Bell) by being more orange-yellow on the lower surface instead of the bright yellow of *nayana*, nor does *nayana* have the blurred appearance of *mulleri*.

From the present information I would like to remove *mulleri* from the synonymy and give it the full specific rank that it deserves.

Mellana fieldi (Bell) 1942

This species was described from Guatemala. In the British Museum there are but three males and a female present and these came from Guatemala. Among the many specimens that I have received from Dr. Escalante for determination were present three males of *fieldi* from Catemaco, Veracruz, collected during December 1963, and one male and two females from Sta. Rosa, Comitán, Chiapas, Mexico, collected during September 1963. These are the first records for the occurrence of *fieldi* in Mexico.

This species bears a slight resemblance to *eulogius* but can readily be separated by the orange-red maculation and orange-red fringes. It is a much darker species on the lower surface of both wings. The genitalia readily separate the two species as well.

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1942. New Records and New Species of Hesperiidæ from Mexico. *Sobret. de los Anales de La Escuela Nacional de Ciencias Biologicas*. Vol. II. No. 4. pp. 455-468.
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1955. A catalogue of the American Hesperiidæ indicating the classification and nomenclature adopted in the British Museum. Part IV, Hesperiiinae and Megathyminae. London: British Museum. 449 pp., pls. 54-88.
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THE GENERIC, SPECIFIC AND LOWER CATEGORY NAMES OF THE NEARCTIC BUTTERFLIES

PART 5 — *The Genus Heliconius*

PADDY McHENRY

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IN ADDITION TO THE GENERIC NAMES given here, the literature includes certain names subjectively synonymous with *Heliconius*. These names have not been included as they are not founded on type species occurring in the Nearctic area nor have they been applied to any of the Nearctic species and, furthermore, *Heliconius* has dating priority over them.

Although I can find no author who has applied it to the Nearctic species, the generic name *Laparus* Billberg has been included in order to provide a replacement for the preoccupied name *Migonitis* Hübner which has been used for certain Nearctic species.

Linnaeus' two spellings for *charitonius* (*emendatio*) have caused some confusion in the literature. This situation is discussed in the data for that name.

LIST OF GENERIC NAMES USED OR AVAILABLE FOR HELICONIUS

HELICONIUS Kluk.

Type. charitonius (Linnaeus).

APOSTAPHIA Hübner.

Type. charitonius (Linnaeus).

HELICONIA Godart.

Type. charitonius (Linnaeus).

HELICONIUS Latreille.

Type. charitonius (Linnaeus).

LAPARUS Billberg.

Type. erato (Linnaeus).

MIGONITIS Hübner.

Type. erato (Linnaeus).

MIGONITIS HÜBNER, 1816, Verz. Bekann. Schmett. (1): 12, no.

1. He included among others: "44. M. erato Linn."

This name is preoccupied by Migonitis Rafinesque, 1815, Analyse: p. 147.

Type. P[apilio]. H[eliconius]. erato Linnaeus, 1758.

Syst. Nat. (10th. ed.). 1: 467, no. 54.

Type Selection, Scudder, [8 Apr.] 1875¹. Proc. Amer. Acad.

Arts Sci. 10: 218-219, no. 698. He said: "Erato may be taken as the type."

LIST OF SPECIES AND LOWER CATEGORY NAMES USED OR AVAILABLE FOR HELICONIUS

1. HELICONIUS CHARITONIUS (LINNAEUS).

charitonius (Linnaeus).

tuckeri Comstock and Brown.

vazquezae Comstock and Brown.

2. HELICONIUS PETIVERANUS (DOUBLEDAY).

petiveranus (Doubleday).

1. HELICONIUS CHARITONIUS (LINNAEUS).

charitonius, P[apilio]. H[eliconius]. (emendatio) Linnaeus.

1767, Syst. Nat. (12th. ed.). 1(2): 757, no. 65; p.

[1339], no. 65. "Habitat in America". No sex, series nor date data given. The name was given as charithonia on page 757 and as charitonia on page [1339]. As first revisors, Comstock and Brown (16 Oct. 1942, Amer. Mus. Nov. (1467): 1-2) selected charitonia as the proper spelling. Correct Latin grammar would seem to dictate the spellings charitonius and charithonius for use with either Papilio or Heliconius as they are both masculine. Maynard, 1891, Butt. N. Engl. (2nd. ed.): pl. 10 explanation page, for fig. 8, gave the name as Heliconia charionia, in error.

tuckeri, Heliconius charitonius W. P. Comstock and F. M. Brown.

16 Oct. 1950, Amer. Mus. Nov. (1467): fig. 3, no. F;

p. 13, no. F; pp. 15-16; p. 19 (in pt.). "Holotype,

Male: Winter Park, Florida, October 4". "Allotype,

Female: Key Largo, Florida, July 15". "Paratypes: One

hundred and twenty-five males and 99 females, all from Florida and Georgia". "The holotypes and allotypes of

HELICONIUS KLUK, 1802, Zwiery, Hist. Nat. Pocz. Gospod.
4: 82-84, no. 143. He included among others:

"17. - charitonia". Heliconius Kluk was included in
the Official List Gen. Names Zool. (1): 126, no. 923.
Hemming, 1958.

Type. P[apilio]. H[eliconius]. charitonius (emendatio)
Linnaeus, 1767, Syst. Nat. (12th. ed.). 1(2): 757, no.
65.

Type Selection, Hemming, Oct. 1933, Entomologist, 66(845):
223. He said: "Type = Heliconius charitonia Linn., Kluk."

APOSTRAPHIA HUBNER, 1816, Verz. Bekann. Schmett. (1): 13, no.
3. He included among others: "58. A. Charitonia Linn.,."

Type. P[apilio]. H[eliconius]. charitonius (emendatio)
Linnaeus, 1767, Syst. Nat. (12th. ed.). 1(2): 757, no.
65.

Type Selection, Scudder, [8 Apr.] 1875¹, Proc. Amer. Acad.
Arts Sci. 10: 116, no. 106. He said: "Charithonia may
be taken as type."

HELICONIA GODART, 1819, In Godart and Latreille in Latreille.
Ency. Meth. 9(1): 203-226. He included among others:

"22... Heliconia Charithonia."

Type. P[apilio]. H[eliconius]. charitonius (emendatio)
Linnaeus, 1767, Syst. Nat. (12th. ed.). 1(2): 757, no.
65.

Type, Selection, Hemming, Oct. 1933, Entomologist, 66(845):
223. He said: "Type = Heliconia charitonia Linn., God."

HELICONIUS LATREILLE, 1804, Nouv. Dict. Hist. Nat.

24(Tab. Meth. Ins.): 185, 199. He included only:

"Papilio ricini, charitonia Fab." which were originally
of Linnaeus. This name is both a homonym and synonym of
Heliconius Kluk.

Type. P[apilio]. H[eliconius]. charitonius (emendatio)
Linnaeus, 1767, Syst. Nat. (12th. ed.). 1(2): 757, no.
65.

Type Selection, Hemming, Sept. 1933, Entomologist, 66(844):
198. He said: "Type = Heliconius charitonia Fab. (= charithonia Linn.)."

LAPARUS BILLBERG, 1820, Enum. Ins. Museo Billberg: p. 77.

He included among others: "Doris... Linn." which is
considered by Hemming (1934, p. 56, no. 102) as a
synonym of P. H. erato Linnaeus, 1758.

Type. P[apilio]. H[eliconius]. erato Linnaeus, 1758.
Syst. Nat. (10th. ed.). 1: 467, no. 54.

Type Selection, Hemming, 1934, Entomologist, 67: 37. He
said: "Type - Papilio doris Linn., 1771 (= Papilio
erato Linn., 1758)."

all new subspecies [described in Comstock's and Brown's paper] are in the collection of the American Museum of Natural History". Mather and Mather. 6 June 1958. Tulane Studies Zool. 6(2): 69, no. 10, spelled as tucgeri, in error.

vazquezae, Heliconius charitonius W. P. Comstock and F. M. Brown, 16 Oct. 1950. Amer. Mus. Nov. (1467): fig. 3, no. 6; p. 13, no. 6; p. 16; p. 19 (in pt.). "Holotype, Male: Campeche, Mexico, November". "Allotype, Female: Allende, Vera Cruz, Mexico, July". "Paratypes: Eighty-four males and 53 females, all from Mexico and Texas". The three Texas specimens are: one male, Sarita, Willacy County; one female, Corpus Christi, Nueces County; one female, New Braunfels, Comal County."

2. HELICONIUS PETIVERANUS (DOUBLEDAY).

petiverana, Hel[iconia]. Doubleday. [4 Aug. 1847]².

In Doubleday and Westwood. Genera Diurn. Lepid. 1(10): 103, no. 18. "Mexico, Honduras." No sex, series nor date data given. The author cited fig. 2, pl. 4, in Petiver's Gazophylacium (1702-11). The name is modified to petiveranus when transferred to the genus Heliconius for purposes of Latin grammar.

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Hemming, F. 1934. Generic Names Holarct. Butt. 1: i-vii, 1-184.

FOOTNOTES

1. A copy of the work among the separates at the Allan Hancock Library (Univ. Sou. Calif.) (ex library, Boston Soc. Nat. Hist.) has the following printed label on the front wrapper: "Library of the Cambridge Entomological Club. Received April 8, 1875, by gift from the author."
2. Hemming. 1936-1943. Jour. Soc. Bibliog. Nat. Hist. 1: 335-464. Gave publication dates for the Genera Diurn. Lepid.

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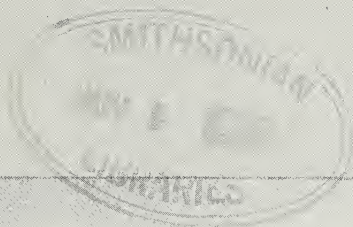
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IN THIS ISSUE

- | | | |
|---|-------------------------------------|----|
| Spring Moths of a Natural Area in Northeastern Kansas | Noel McFarland | 1 |
| A New Species of <i>Nepticula</i> on Bur Oak in Ontario | T. N. Freeman | 19 |
| Fixation of the Type Locality of <i>Lycaena phlaeas</i>
<i>hypophlaeas</i> and a Foodplant Correction | Oakley Shields | 22 |
| Description of a New Species of <i>Xylomiges</i> from California | John S. Buckett | 23 |
| The Life-Histories of South African <i>Colotis erone</i> , <i>C. ione</i> ,
<i>C. vesta</i> and <i>Leptosia alcesta</i> (Pieridae) | Gowan C. Clark and C. G. C. Dickson | 31 |
| A New Species of <i>Feralia</i> | John S. Buckett | 43 |
| Homonymy of the "New Genus" <i>Petaluma</i> and Proposal of
the Name <i>Petalumaria</i> | J. S. Buckett and W. R. Bauer | 52 |
| Rearing <i>Euleucophaeus rubridorsa</i> and <i>E. lex</i> | Brian O. C. Gardiner | 53 |
| The Status of Some HesperIIDae from Mexico | H. A. Freeman | 59 |
| The Generic, Specific and Lower Category Names of the
Nearctic Butterflies | Paddy McHenry | 65 |

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HILLTOPPING

AN ECOLOGICAL STUDY OF
SUMMIT CONGREGATION BEHAVIOR
OF BUTTERFLIES ON A
SOUTHERN CALIFORNIA HILL

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San Diego, Calif.*

THE LEPIDOPTERA RESEARCH
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FOREWORD

"Territoriality" in various vertebrate animals has been studied for many years, involving not only the fact that territoriality exists as a behavior pattern but also involving a functional need for this behavior in the life history of the animal. "Hilltopping" of butterflies as a form of territoriality has been observed by all persons who have collected, or studied, these invertebrates in the field, but no one has made such a concerted effort at obtaining analytical data as has Mr. Oakley Shields. All experimental and/or analytical studies represent an effort on the part of a worker at obtaining significant data upon which to draw conclusions; there are apt to be as many different conclusions derived from the same set of data as there are independent analyses made of them but we can be sure that Mr. Shields has made every effort at drawing conclusions in keeping with the data he has presented. Others may be able to draw other conclusions from the same data. This is in the fulfillment of scientific spirit, and is as it should be. Mr. Shields has also given a very complete Bibliography of work related to this field. The literature of entomology is extremely large and he is to be commended for his efforts; such omissions as have occurred should be considered in the context that it could happen to any of us.

The Lepidoptera Research Foundation, Inc. is proud to be able to present this work of Mr. Oakley Shields in complete form in the thought that in this way it will prove to be more usable and satisfactory than if it were divided into sections for publication.

William Hovanitz
Editor

TABLE OF CONTENTS

ABSTRACT	71
INTRODUCTION	73
MATERIALS AND METHODS	89
Location and description of study area	91
RESULTS	93
Species present	93
Territorial and aggressive behavior	96
Daily residence	105
Diurnal periodicity	109
Migration	112
Mark-recapture study	112
<i>Papilio zelicaon</i> release experiments	117
Percent virginity	122
Female rarity	128
Female behavior and mating	133
Behavior of sexes after uncoupling	141
Larval foodplant proximity	141
Species approach to the summit	144
Effects of wind at the summit	145
Feeding	146
Roosting	147
Predation	148
DISCUSSION	149
CONCLUSIONS	164
ACKNOWLEDGEMENTS	166
LITERATURE CITED	168

ABSTRACT

IT IS WIDELY KNOWN that butterflies often congregate in numbers on the summits of hills, ridges, peaks, and mountain-tops. However, few investigations have been made to determine why this behavior has developed. This study was conducted to try to answer this question.

Initially, purely observational work was necessary to adequately describe the phenomenon. Dictionary Hill near Spring Valley, San Diego County, California, was chosen as the primary study area because it was readily accessible and the surrounding area was relatively undisturbed by man. To follow the behavior of individuals, a mark-release program was established. It was

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found that the summit population consisted primarily of males that exhibited territorial or pathway-patrol behavior, with aggression displayed toward other butterflies. These males sometimes spent most of the day in such behavior and repeatedly returned to the summit on subsequent days. During the study 21 species were found to congregate on the summit, while another 25 species flew "up-and-over" the summit without congregating or were generally distributed over the entire hill.

Certain insects are known to congregate at topographic summits to facilitate mating. To test this hypothesis for butterflies, the behavior of females that approached the summit was observed and females were collected. An abnormally high percentage of females captured on the summit was virgin when compared to those captured elsewhere. This fact was determined by the absence of a spermatophore in the female's bursa copulatrix. Also, a substantial number of summit matings was observed for two species on the summit. The apparent scarcity of females was due to the inconspicuousness of *in copula* pairs and due to the fact that virgins stayed only long enough to mate and non-virgins only rarely approached the summit. Virgin females lingered about the summit until mated and readily mated with courting males. Females of two species were seen to depart from the summit after mating.

Further evidence that this phenomenon serves to bring males and females together to insure fertilization comes from an experiment in which mated and unmated females of one species, *Papilio zelicaon*, were released away from the hill. Only the unmated females were later captured on the summit, indicating that virgin females seek the summit. Evidence that males actively seek the summit comes from the fact that a substantial number of male *P. zelicaon* released at various directions and distances away from the hill later returned to the summit.

The evidence strongly indicates that "hilltopping" in butterflies is a phenomenon in which males and virgin (or multiple-mating) females instinctively seek a topographic summit to mate. The selective advantage presumably would be to centralize isolated populations for mating and thus stabilize the gene pool. Other possible alternative explanations have been advanced in the literature but all are here shown to be highly unlikely. The strongest alternative theory, that butterflies are concentrated on summits due to winds and updrafts, is shown to be unsatisfactory.

Observations on feeding, roosting, and predation of hilltopping butterflies are also included, and the phenomenon is discussed in relation to hilltopping insects.

INTRODUCTION

Students of insect behavior are aware that insects are largely at the mercy of their instincts. Insects do not behave a certain way because it is fun or because they want to but do so because their instincts compel them to. Thus when one sees butterflies flying about the summit of a hill and "playing tag" with each other, one may wonder what instinct brought them there and why the habit developed. This study was conducted to determine the reasons for this summit congregation behavior in butterflies.

Swarms of insects on the summits of ridges, hills, and mountains are frequently mentioned in the literature (Slosson, 1893, 1894, 1895; Bowditch, 1896; Guppy, 1897; Newcomb, 1901; Currie, 1904; Poulton, 1904; Hudson, 1905; Meinecke, 1917; Howard, 1918; Van Dyke, 1919; Bryan, 1923, 1926; Scott, 1926; Swezey and Williams, 1932; Alexander, 1940; Chapman, 1954a; Edwards, 1956, 1957b, 1960, 1961; Mani, 1962). Sometimes large numbers of different insects are found dead on snow at summits (Bowditch, 1896; Caudell, 1903; Currie, 1904; Bryan, 1917, 1923; Meinecke, 1917; Fletcher, 1964:141). Such swarms are often composed almost entirely or exclusively of males that are congregating on a prominence from the surrounding territory (see, for example, Chapman, 1954a; Dodge & Seago, 1954; Catts, 1964; Shepard, 1966). Groups frequenting summits include the orders Coleoptera, Diptera, Hymenoptera, and Lepidoptera (Table 1). A number of Lepidoptera families contain species that show

TABLE 1. Families of insects with species
that are known to hilltop

Family	Sources
COLEOPTERA	
Byrrhidae	Edwards, 1956
Cerambycidae	Poulton, 1904
Chysomelidae	Slosson, 1893; Van Dyke, 1919
Coccinellidae	Slosson, 1893; Poulton, 1904; Hudson, 1905; Van Dyke, 1919; Bryan, 1926; Balduf, 1935; Chapman, 1954a; Chapman, Romer, and Stark, 1955; Edwards, 1956, 1957a; Hagen, 1962
Elateridae	Edwards, 1956
Scarabaeidae	Hudson, 1905
Rhynchophora	Van Dyke, 1919
DIPTERA	
Agromyzidae	Bryan, 1926
Anthomyidae	Bryan, 1926
Bibionidae	Hudson, 1905
Bombyliidae	Currie, 1904; Van Dyke, 1919; Chap- man, 1954a; Dodge and Seago, 1954; Edwards, 1956, 1957b
Borboridae	Bryan, 1926
Calliphoridae	Dodge and Seago, 1954; Edwards, 1956
Culicidae	Knab, 1907
Cuterebridae	Chapman, 1954a; Catts, 1963
Gastrophilidae	Walton, 1930; Grunin, 1959
Hypodermatidae	Grunin, 1959
Muscidae	Bryan, 1926; Scott, 1926; Dodge and Seago, 1954; Edwards, 1957b
Oestridae	Aldrich, 1915; Grunin, 1959; Catts 1964
Phoridae	Dodge and Seago, 1954
Rhagionidae	Shemanchuk and Weintraub, 1961
Sarcophagidae	Chapman, 1954a; Dodge and Seago, 1954; Edwards, 1956, 1957b; Grunin, 1959
Simuliidae	Edwards, 1956
Syrphidae	Currie, 1904; Van Dyke, 1919; Bryan, 1926; Chapman, 1954a; Dodge and Seago, 1954; Edwards, 1956, 1960
Tabanidae	Chapman, 1954a; Dodge and Seago, 1954; Edwards, 1956, 1957b
Tachinidae	Currie, 1904; Van Dyke, 1919; Bryan, 1926; Chapman, 1954a; Edwards, 1956, 1960
HYMENOPTERA	
Formicidae (winged ants only)	Poulton, 1904; Hudson, 1905; Wheeler, 1905, 1917a; Van Dyke, 1919; Scott, 1926; Gregg, 1947; Michener, 1948; Chapman, 1954b; Fosberg, 1955; Chapman, 1957
Ichneumonidae	Slosson, 1894; Bryan, 1926; Chapman, 1954a
Psammocharidae	Bryan, 1926
Siricidae	Scott, 1923, 1924, 1926; Walsh, 1924; Chapman, 1954a; Edwards, 1957b
Sphecidae	Poulton, 1904

hilltopping activity: Hesperiididae, Lycaenidae, Nymphalidae, Papilionidae, and Pieridae (Table 2). Welling (1958) reported the phenomenon in some nocturnal moths on a hill in Ohio. Certain hibernating Coccinellidae, Chrysomelidae, and Rhyncho-phora beetle aggregations (Van Dyke, 1919; Chapman, 1954a) and aestivating Noctuidae moth aggregations (Common, 1952) have been reported from summits; such aggregations were not composed predominantly of males. The explanation of this phenomenon of insects congregating on summits, known as "hilltopping" in butterfly literature, is known for certain insects but remains unsettled for butterflies.

Butterfly collectors often find that hilltops are profitable places to collect. Certain species that are rare or apparently absent in the surrounding countryside may congregate at such places in numbers (Van Someren, 1955). Barrett and Burns (1951:4-5), in referring to males of many species of hesperiids and lycaenids in Australia and New Guinea, said that certain hilltops will always have particular species at the proper time of year. Knudsen (1954) found three species of butterflies abundant on Kennesaw Mountain, Georgia. Here he found on the summit several hundred butterflies in an area of a few hundred square feet. On two hilltops in Australia, Waterhouse (1932:267) found butterflies clustered by the hundreds just before dusk or on the lee side of a shrub during wind. Minimum distances traveled by hilltopping butterflies from the nearest areas of their foodplants are reported as several thousand vertical feet for *Papilio indra kaibabensis* in Arizona (Emmel & Emmel, 1967) and 1,700 vertical meters for *Pieris callidice* in France (Muspratt, 1954).

Various theories have been proposed for hilltopping among insects. Poulton (1904) discussed insects in general that frequent summits and concluded that they seek "conspicuous isolated features in the landscape" to mate, thus greatly reducing the area in which sexual encounters could occur. He offered as supporting evidence the ceramycid *Dorcadion* "pairing freely" on a summit. This theory has been particularly substantiated by work with winged ants and bot flies: observations by Forel (1874), Michener (1948), Fosberg (1955), and Chapman (1957) refer to matings among summit swarms of winged ants; bot flies on summits were reported to mate by Walton (1930), Grunin (1959), and Catts (1963, 1964). Dodge and Seago (1954) reported twenty-one mating pairs of Diptera from mountain summits of Georgia, and Chapman (1954a) mentioned

TABLE 2. A list of known butterfly
"hilltopping" species

Species	Realm	Sources
PAPILIONIDAE		
Papilioninae		
<u>Battus philenor</u>	Nea.	Weiss, 1927; Merritt, 1952
<u>B. polydamus</u>	Neo.	new (Brown)
<u>Chilasa clytia</u>	Ori.	Tinkham, 1937; Best, 1954; Wynter-Blyth, 1957
<u>C. c. dissimilis</u>	Ori.	Best, 1954
<u>Graphium</u> , most spec.	Neo.	new (Brown)
<u>G. marcellus</u>	Nea.	Merritt, 1952; Knudsen 1954
<u>Papilio</u> , many spec.	Neo.	new (Brown)
<u>P. anactus</u>	Aus.	new (Wyatt)
<u>P. anchisiades</u>	Neo.	new (Brown)
<u>P. androgeus</u>	Neo.	new (Brown)
<u>P. angolanus</u>	Eth.	Van Someren, 1955
<u>P. arcturus</u>	Ori.	Wynter-Blyth, 1957
<u>P. bairdii</u>	Nea.	Grinnell and Grinnell, 1907 new (many)
<u>P. b. brucei</u>	Nea.	Rodeck, 1950; Newcomer, 1967
<u>P. brevicauda</u>	Nea.	Edwards, 1884; Tilden, 1964
<u>P. crino</u>	Ori.	Best, 1954
<u>P. demodocus</u>	Eth.	Longstaff, 1912:225; Van Someren, 1955
<u>P. demoleus</u>	Eth.	Trimen, 1889
<u>P. eurymedon</u>	Nea.	Edwards, 1887; Merritt, 1952; Garth and Tilden, 1963
<u>P. feisthamelii</u>	Pal.	new (Wyatt)
<u>P. glaucus</u>	Nea.	Scudder, 1887, 1889; Weed, 1901; Longstaff, 1912: 149; Weiss, 1927; Merritt, 1952
<u>P. g. arcticus</u>	Nea.	Wyatt, 1957a
<u>P. hector</u>	Ori.	Longstaff, 1912: 380
<u>P. indra</u>	Nea.	Mead, 1878; Edwards, 1884; Wright, 1906; Newcomer, 1910; Martin and Ingham, 1930; Garth, 1934; Emmel and Emmel, 1962; Garth and Tilden, 1963
<u>P. indra fordi</u>	Nea.	new (many)
<u>P. i. kaibabensis</u>	Nea.	Emmel and Emmel, 1967
<u>P. i. martini</u>	Nea.	Emmel and Emmel, 1968
<u>P. i. minori</u>	Nea.	Eff, 1962
<u>P. i. pergamus</u>	Nea.	new (many)

TABLE 2 (continued)

Species	Realm	Sources
<u>Papilio leonidas</u>	Eth.	Van Someren, 1955
<u>P. liomedon</u>	Ori.	Wynter-Blyth, 1957
<u>P. machaon</u>	Pal.	Seitz, 1909; Longstaff, 1912:46; deRhe-Philipe, 1932; Muspratt, 1954; Wynter-Blyth, 1957
<u>P. m. aliaska</u>	Nea.	Cary, 1907; Leussler, 1935; Rawson, 1955; Wyatt, 1957a
<u>P. m. asiatica</u>	Pal.	Hayward, 1937
<u>P. m. centralis</u>	Pal.	Peile, 1923
<u>P. m. hippocrates</u>	Pal.	Longstaff, 1912:46
<u>P. macleayanus</u>	Aus.	Waterhouse, 1932; new (Wyatt)
<u>P. paris</u>	Ori.	Wynter-Blyth, 1957
<u>P. pelaus</u>	Neo.	New (Turner)
<u>P. podalirius</u>	Pal.	Seitz, 1909; Muspratt, 1954
<u>P. polymetus</u>	Neo.	new (Kesselring)
<u>P. polyxenes asterius</u>	Nea.	Weed, 1901; Weiss, 1927; Clark, 1932; Merritt, 1952; Knudsen, 1954; Tilden, 1964
<u>P. rex</u>	Eth.	Van Someren, 1955
<u>P. rudkini</u>	Nea.	new (many)
<u>P. rutulus</u>	Nea.	new (Guppy, Scott, Tilden)
<u>P. thersites</u>	Neo.	Avinoff and Shoumatoff, 1946; Shoumatoff, 1953; new (Turner)
<u>P. thoas</u>	Neo.	new (Brown)
<u>P. torquatus</u>	Neo.	new (Brown)
<u>P. troilus</u>	Nea.	Weiss, 1927, 1928
<u>P. zelicaon</u>	Nea.	Mead, 1878; Osten-Sacken, 1882; Edwards, 1887; Snyder, 1894; Wright, 1906; Newcomer, 1910; Grinnell, 1915; Whitehouse, 1918; Van Dyke, 1919; Comstock, 1927; Garth, 1935; Merritt, 1952; Guppy, 1953; Emmel and Emmel, 1962; Garth and Tilden, 1963; Tilden, 1964
<u>Papilio zelicaon-polyxenes hybrid (nitra)</u>	Nea.	new (Scott)

TABLE 2 (continued)

Species	Realm	Sources
<u>Teinopalpus</u> <u>imperialis</u>	Ori.	Seitz, 1927; Parsons, 1948; Bailey, 1951; Saunders, 1955; Wynter- Blyth, 1957
<u>Zetides cloanthus</u>	Ori.	Bailey, 1951; Wynter- Blyth, 1957
PIERIDAE		
Coliadinae		
<u>Eurema hecabe</u>	Pal. Ori.	Longstaff, 1912:46, 388
<u>Phoebis</u> spp.	Neo.	new (Kesselring)
Pierinae		
<u>Anthocaris belia</u>	Pal.	Gurney, 1907
<u>A. cethura</u>	Nea.	Morrison, 1883; Comstock, 1927; Garth, 1934
<u>A. falloui</u>	Pal.	Fountaine, 1906
<u>A. midea</u>	Nea.	Rawson, 1951; Arnhold, 1952; Merritt, 1952; Shoumatoff, 1953; Knud- sen, 1954
<u>A. pima</u>	Nea.	Beutenmuller, 1898; Wright, 1906; Comstock, 1927
<u>A. tagis</u>	Pal.	Gurney, 1907
<u>Colotis bowkeri</u>	Eth.	Trimen, 1889
<u>C. eris</u>	Eth.	Trimen, 1889
<u>Daptonoura</u> spp.	Neo.	new (Kesselring)
<u>Delias harpalyce</u>	Aus.	new (Wyatt)
<u>D. nysa</u>	Aus.	new (Wyatt)
<u>Euchloe ausonides</u> <u>coloradensis</u>	Nea.	Garth, 1934, 1935; Garth and Tilden, 1963
<u>E. belemia</u>	Pal.	Longstaff, 1912:162; Peile, 1923
<u>E. belledice</u>	Pal.	Longstaff, 1912:162
<u>E. charlonia</u>	Pal.	Longstaff, 1912:162; Dover, 1922; Wynter- Blyth, 1957
<u>E. c. transcaspica</u>	Pal.	Peile, 1923
<u>E. hyantis</u>	Nea.	Garth, 1934, 1935; Garth and Tilden, 1963
<u>E. h. lotta</u>	Nea.	Garth, 1934, 1935
<u>E. olympia</u>	Nea.	Clark and Clark, 1951; Arnhold, 1952; Merritt, 1952
<u>E. o. rosa</u>	Nea.	new (Justice)
<u>Piercolias huanaco</u>	Neo.	Seitz, 1924
<u>Pieris callidice</u>	Pal.	Muspratt, 1954
<u>P. daplidice</u>	Pal.	Longstaff, 1912:33
<u>P. occidentalis</u>	Nea.	Snyder, 1894; Dod, 1908a; Shepard, 1966
<u>P. o. calyce</u>	Nea.	new (many)

TABLE 2 (continued)

Species	Realm	Sources
<u>Pieris protodice</u>	Nea.	new (many)
<u>P. rapae</u>	Nea., Aus.	Scudder, 1887, 1889; Meinecke, 1917; Bryan, 1926
<u>P. sisymbrii</u>	Nea.	Tilden, 1964; new (many)

NYMPHALIDAE

Danaeinae

<u>Ceratinia vallonina</u>	Neo.	new (Kesselring)
<u>Chittira fumata</u>	Ori.	Longstaff, 1912:388
<u>Euploea diocletiana</u>	Ori.	Rawlins, 1949
<u>Ideopsis gaura</u>		
<u>parakana</u>	Ori.	Rawlins, 1949
<u>Mechanitis nessaea</u>	Neo.	new (Kesselring)
<u>Thyridia singularis</u>	Neo.	new (Kesselring)

Satyrinae

<u>Neominois ridingsii</u>	Nea.	Comstock, 1927
<u>Oeneis chryxus</u>	Nea.	Snyder, 1894, 1897; McDunnough, 1927
<u>O. c. ivallda</u>	Nea.	Wright, 1906; Grinnell, 1915; Comstock, 1927; Martin and Ingham, 1930; Tilden, 1959; Garth and Tilden, 1963; Brown, 1965
<u>O. c. stanislaus</u>	Nea.	new (many)
<u>O. marcounii</u>	Nea.	Elwes and Edwards, 1893; Masters et al., 1967
<u>O. melissa assimilis</u>	Nea.	Freemen, 1948; Munroe 1951
<u>O. m. beanii</u>	Nea.	Elwes and Edwards, 1893; Dod, 1901, 1908a, 1908b; Fletcher, 1905; Nicholl, 1906; Fletcher and Gibson, 1908; Whitehouse, 1918; McDunnough, 1927
<u>O. m. lucilla</u>	Nea.	Mead, 1875; new (many)
<u>O. nevadensis</u>	Nea.	Edwards, 1887; Danby, 1894; Fletcher, 1906; Wright, 1906; Guppy, 1962
<u>O. n. iduna</u>	Nea.	Edwards, 1884
<u>O. polixenes brucei</u>	Nea.	Klots, 1937
<u>Pararge hindukushica</u>	Pal.	new (Wyatt)
<u>P. megaera</u>	Pal.	Fountaine, 1906; Peile, 1923; Scott, 1926; Temple, 1953; Muspratt, 1954
<u>P. menava</u>	Pal.	new (Wyatt)

TABLE 2 (continued)

Species	Realm	Sources
<u>Pararge moera</u>	Pal.	new (Wyatt)
<u>Pharneuptychia</u> spp.	Neo.	new (Brown)
Morphinae		
<u>Brassolis</u> spp.	Neo.	new (Brown)
<u>Caligo</u> spp.	Neo.	new (Brown)
<u>Catoblepia</u> spp.	Neo.	new (Brown)
<u>Dasyophthalma</u> spp.	Neo.	new (Brown)
<u>Dynastor darius</u>	Neo.	new (Brown)
<u>Eryphanis</u> spp.	Neo.	new (Brown)
<u>Narope</u> spp.	Neo.	new (Brown)
<u>Opsiphanes</u> spp.	Neo.	new (Brown)
Charaxinae		
<u>Agrias</u> spp.	Neo.	new (Brown)
<u>Anaea</u> , most species	Neo.	new (Brown)
<u>A. ryphae</u>	Neo.	new (Kesselring)
<u>Charaxes achaemenes</u>	Eth.	Van Someren, 1955
<u>C. castor</u>	Eth.	Van Someren, 1955
<u>C. epijasius</u>	Eth.	Van Someren, 1955
<u>C. fabius</u>	Ori.	Best, 1953, 1954
<u>C. polyena imna</u>	Ori.	Best, 1953, 1954
<u>C. viola</u>	Eth.	Van Someren, 1955
<u>Eriboea athamas</u>	Ori.	Best, 1953, 1954
<u>E. pyrrhus sempronius</u>	Aus.	new (Wyatt)
<u>Euxanthe</u> spp.	Eth.	Van Someren, 1955
<u>Hamamumida daedulus</u>	Eth.	Trimen, 1887; Van Someren, 1955
<u>Prepona</u> , most species	Neo.	new (Brown)
<u>P. demophon</u>	Neo.	new (Kesselring)
<u>Siderone nemesis</u>	Neo.	new (Kesselring)
<u>Zaretas isidora</u>	Neo.	new (Kesselring)
Nymphalinae		
<u>Adelpha</u> , many spec.	Neo.	new (Brown)
<u>Ageronia februa</u>	Neo.	new (Kesselring)
<u>A. feronia</u>	Neo.	new (Kesselring)
<u>Argynnis hyperbius</u>	Pal., Ori.	Longstaff, 1912:100; Fraser, 1916; Wynter- Blyth, 1957
<u>A. lathonia</u>	Pal.	Wynter-Blyth, 1957
<u>A. l. issaea</u>	Pal.	Longstaff, 1912:46, 64; Seitz, 1927
<u>Boloria alberta</u>	Nea.	Dod, 1901, 1908b; Nicholl, 1906; Wyatt, 1957b
<u>B. astarte</u>	Nea.	Dod, 1901, 1908a; Fletcher, 1905; Nicholl, 1906; Skinner, 1908; Whitehouse, 1918; Wyatt, 1957b

TABLE 2 (continued)

Species	Realm	Sources
<u>Boloria polaris</u>	Nea.	Munroe, 1951
<u>gronlandica</u>		
<u>B. selene myrina</u>	Nea.	Scudder, 1887, 1889
<u>B. toddi</u>	Nea.	Scudder, 1887, 1889
<u>Chlosyne californica</u>	Nea.	new (many)
<u>C. ismeria</u>	Nea.	Knudsen, 1954
<u>C. i. carlota</u>	Nea.	new (Justice, Scott)
<u>C. leanira wrightii</u>	Nea.	new (Breedlove)
<u>C. theona</u>	Nea.	new (Shields)
<u>Doxocopa agathina</u>	Neo.	new (Brown)
<u>D. kallima</u>	Neo.	new (Brown)
<u>D. vacuna</u>	Neo.	new (Brown)
<u>D. zunilda</u>	Neo.	new (Brown)
<u>Dynamine mylitta</u>	Neo.	new (Brown)
<u>D. argyrippa</u>	Neo.	new (Brown)
<u>Eueides isabella</u>	Neo.	new (Brown)
<u>Euphydryas anicia</u>	Nea.	Whitehouse, 1918
<u>E. a. alena</u>	Nea.	new (Scott)
<u>E. a. brucei</u>	Nea.	new (Justice)
<u>E. a. capella</u>	Nea.	new (Scott)
<u>E. a. eurytion</u>	Nea.	new (Scott)
<u>E. chalcedona</u>	Nea.	new (many)
<u>E. c. sierra</u>	Nea.	Brown, 1965
<u>E. editha</u>	Nea.	new (Scott, Thorne)
<u>E. e. nubigena</u>	Nea.	new (many)
<u>Euripus consimilis</u>	Ori.	Wynter-Blyth, 1957
<u>Hestina nama</u>	Ori.	Bailey, 1951
<u>Historis spp.</u>	Neo.	new (Brown)
<u>H. odius</u>	Neo.	Avinoff and Shoumatoff, 1946
<u>H. orion</u>	Neo.	new (Kesselring)
<u>Limenitis archippus</u>	Nea.	Scudder, 1887, 1889
<u>L. arthemis</u>	Nea.	Scudder, 1887, 1889
<u>L. astyanax</u>	Nea.	Weiss, 1927
<u>L. lorquini</u>	Nea.	Martin and Ingham, 1930
<u>Melitaea didyma</u>	Pal.	Peile, 1923
<u>M. trivia</u>	Pal.	Peile, 1923
<u>M. t. perseia</u>	Pal.	Peile, 1923
<u>Myscelia sophronia</u>	Neo.	new (Brown)
<u>M. orsis</u>	Neo.	new (Brown)
<u>Nymphalis antiopa</u>	Nea.	Scudder, 1887, 1889
		Weiss, 1927
<u>N. californica</u>	Nea.	new (Breedlove, Dvorak)
<u>N. cashmiriensis</u>	Pal.	Longstaff, 1912:46
<u>N. milberti</u>	Nea.	Scudder, 1863, 1887, 1889; Weed, 1901; Weiss, 1927; Garth, 1935; Garth and Tilden, 1963
<u>N. urticae</u>	Pal.	Muspratt, 1954
<u>N. vau-album j-album</u>	Nea.	Scudder, 1887, 1889; Weiss, 1927

TABLE 2 (continued)

Species	Realm	Sources
<u>Phyciodes tharos</u>	Nea.	Scudder, 1887, 1889
<u>Poladryas pola</u>	Nea.	new (Scott, Shields)
<u>P. p. arachne</u>	Nea.	new (Scott)
<u>Polygonia egea</u>	Pal.	Wynter-Blyth, 1957
<u>P. faunus</u>	Nea.	Scudder, 1863, 1874, 1887, 1889
<u>P. gracilis</u>	Nea.	Scudder, 1887, 1889
<u>P. interrogationis</u>	Nea.	Morrison, 1874; Scudder, 1887, 1889
<u>Precis, 3 species</u>	Eth.	Van Someren, 1955
<u>P. orithyia</u>	Pal.	Longstaff, 1912:46
<u>Speyeria atlantis</u>	Nea.	Scudder, 1887, 1889
<u>S. callippe comstocki</u>	Nea.	new (many)
<u>S. c. meadii</u>	Nea.	new (Scott)
<u>S. c. nevadensis</u>	Nea.	new (Shields)
<u>S. coronis halcyone</u>	Nea.	new (Scott)
<u>S. edwardsii</u>	Nea.	new (Scott)
<u>S. egleis linda</u>	Nea.	new (Ellis)
<u>S. e. tehachapina</u>	Nea.	Comstock, 1927; Emmel and Emmel, 1963a
<u>S. hydaspe</u>	Nea.	Shepard, 1966
<u>S. mormonia</u>	Nea.	Shepard, 1966
<u>S. zerene bremnerii</u>	Nea.	Edwards, 1887
<u>S. z. platina</u>	Nea.	new (Ellis)
<u>Vanessa atalanta</u>	Nea., Neo., Pal.	Mead, 1892; Dison, 1922; Moffat, 1922; Martin and Ingham, 1930; Shoumatoff, 1953; Muspratt, 1954; Emmel and Emmel, 1962
<u>V. cardui</u>	Nea., Pal., Eth., Ori., Aus.	Edwards, 1884; Longstaff, 1912:98, 162, 201, 385, 433; Dixon, 1922; Moffat, 1922; Seitz, 1924; Bryan, 1926; Weiss, 1927; Martin and Ingham, 1930; Tinkham, 1944; Tilden, 1961; Emmel and Emmel, 1962; Moucha, 1963
<u>V. c. kershawi</u>	Aus.	Longstaff, 1912:453
<u>V. caryae</u>	Nea.	Edwards, 1884; new (many)
<u>V. dejeani</u>	Ori.	Seitz, 1927
<u>V. gonerilla</u>	Aus.	Hudson, 1898; Longstaff, 1912:482
<u>V. indica</u>	Ori.	Longstaff, 1912:385
<u>V. itea</u>	Aus.	Hudson, 1898; Longstaff, 1912:448
<u>V. myrinna</u>	Neo.	new (Brown)
<u>V. tameamea</u>	Aus.	Zimmerman, 1958

TABLE 2 (continued)

Species	Realm	Sources
<u>Vanessa virginiensis</u>	Nea.	Mead, 1892; Wright, 1908, 1930; Weiss, 1928; Martin and Ingham, 1930; Richards, 1931; Clark, 1932; Shoumatoff, 1953; Emmel and Emmel, 1962
<u>V. v. brasiliensis</u>	Neo.	new (Brown)
Acraeinae		
<u>Acraea</u> spp.	Eth.	Van Someren, 1955
<u>Actinote</u> , most spec.	Neo.	new (Brown)
LYCAENIDAE		
Riodininae		
many species, nearly 40 on one hilltop in Rio de Janeiro	Neo.	new (Brown)
<u>Dodona ouida</u>	Pal.	Wynter-Blyth, 1957
<u>Nymula calyce</u>	Neo.	new (Brown)
Lycaeninae		
<u>Aphnaeus</u> spp.	Eth.	Van Someren, 1955
<u>Arcas</u> , many species	Neo.	new (Brown)
<u>Argiolaus</u> spp.	Eth.	Van Someren, 1955
<u>Atlides</u> , many species	Neo.	new (Brown)
<u>A. halesus</u>	Nea.	new (many)
<u>Callophrys dumetorum</u>	Nea.	new (Shields, Thorne)
<u>C. viridis</u>	Nea.	new (Gorelick)
<u>Celastrina argiolus</u>		
<u>echo</u>	Nea.	new (Shields)
<u>C. a. ladonidas</u>	Pal.	Longstaff, 1912:142
<u>C. a. pseudargiolus</u>	Nea.	Scudder, 1887, 1889
<u>C. lanka</u>	Ori	Longstaff, 1912:388
<u>C. puspa</u>	Ori.	Wynter-Blyth, 1957
<u>C. singalensis</u>	Pal.	Longstaff, 1912:46
<u>Egumbia</u> spp.	Eth.	Van Someren, 1955
<u>Epamera</u> spp.	Eth.	Van Someren, 1955
<u>Evenus</u> , many species	Neo.	new (Brown)
<u>Everes argiades</u>	Pal.	Muspratt, 1954
<u>E. comyntas</u>	Nea.	Weiss, 1928
<u>E. diporides</u>	Pal.	Wynter-Blyth, 1957
<u>Incisalia eryphon</u>	Nea.	new (Dvorak)
<u>I. fotis</u>	Nea.	new (Henne, Shields)
<u>I. iroides</u>	Nea.	new (Thorne)
<u>I. iroides-fotis</u> (hybrid)	Nea.	new (Henne)
<u>I. niphon</u>	Nea.	Scudder, 1889
<u>Lampides boeticus</u>	Aus.	Bryan, 1926
<u>Lepidochrysops</u> spp.	Eth.	Van Someren, 1955
<u>Leptotes marina</u>	Nea.	new (Shields)
<u>Lycaena sallustius</u>	Aus.	Longstaff, 1912:482

TABLE 2 (continued)

Species	Realm	Sources
<u>Miletis delicia</u>	Aus.	new (Wyatt)
<u>Mitoura spinetorum</u>	Nea.	Shields, 1965
<u>Myrina</u> spp.	Eth.	Van Someren, 1955
<u>Ogyris genoveva</u>	Aus.	new (Wyatt)
<u>Polyommatus baeticus</u>	Pal., Ori.	Longstaff, 1912:64, 388
<u>Pratapa blanka</u>	Ori.	Wynter-Blyth, 1957
<u>Pseudodipsas</u> <u>brisbanensis</u>	Aus.	new (Wyatt)
<u>Satyrium behrii</u>	Nea.	new (Emmel, Scott, Shields)
<u>S. calanus</u>	Nea.	Weiss, 1927
<u>S. saepium</u>	Nea.	new (Emmel, Shields)
<u>S. titus</u>	Nea.	new (Shields)
<u>Spindasis</u> spp.	Eth.	Van Someren, 1955
<u>Strymon columella</u>	Nea.	new (Shields)
<u>S. melinus</u>	Nea.	Tilden, 1964; new (many)
<u>Tajuria</u> spp.	Ori.	Wynter-Blyth, 1957
<u>Talicauda nyseus</u>	Ori.	Longstaff, 1912:98
<u>Thecla</u> spp.	Ori.	Wynter-Blyth, 1957
<u>Theclini</u> , a great number of species	Neo.	new (Brown)
<u>Virachola</u> spp.	Eth.	Van Someren, 1955
<u>V. isocrates</u>	Ori.	Wynter-Blyth, 1957

HESPERIIDAE

Coeliadinae

Bibasis sena

Ori.	Longstaff, 1912:357; Wynter-Blyth, 1957
Eth.	Van Someren, 1955

Coeliades forestansPyrhopyginae

many species

Neo.	new (Brown)
------	-------------

Trapezitinae

"The majority" of 51
species in Australia

Aus.	Waterhouse, 1932
------	------------------

Hesperilla idothea

Aus.	new (Wyatt)
------	-------------

Toxidia peroni

Aus.	new (Wyatt)
------	-------------

Trapezites iacchoides

Aus.	new (Wyatt)
------	-------------

T. iacchus

Aus.	new (Wyatt)
------	-------------

T. phigalia

Aus.	new (Wyatt)
------	-------------

Pyrginae

many crepuscular
species

Neo.	new (Brown)
------	-------------

Astrartes spp.

Neo.	new (Brown)
------	-------------

Baracus vittatus

Ori.	Longstaff, 1912:388
------	---------------------

Celaenorrhinusambareesa

Ori.	Longstaff, 1912:391
------	---------------------

Epargyreus spp.

Neo.	new (Brown)
------	-------------

Erynnis afranius

Nea.	Snyder, 1894 (as lucilius); Emmel and Emmel, 1962
------	--

E. brizo

Nea.	new (Scott)
------	-------------

TABLE 2 (continued)

Species	Realm	Sources
<u>Erynnis brizo burgessi</u>	Nea.	Freeman, 1951
<u>E. b. lacustra</u>	Nea.	new (many)
<u>E. horatius</u>	Nea.	new (Scott)
<u>E. icelus</u>	Nea.	Scudder, 1887, 1889; Tilden, 1964; new (Scott)
<u>E. martialis</u>	Nea.	new (Scott)
<u>E. meridianus</u>	Nea.	Freeman, 1951
<u>E. pacuvius</u>	Nea.	Grinnell, 1904; new (Shields)
<u>E. p. callidus</u>	Nea.	Grinnell, 1904; new (Shields)
<u>E. p. pernigra</u>	Nea.	new (La Due, MacNeill)
<u>E. persius fredericki</u>	Nea.	new (Scott, Shields)
<u>E. propertius</u>	Nea.	new (Shields)
<u>E. telemachus</u>	Nea.	new (Scott)
<u>E. tristis</u>	Nea.	Freeman, 1951; new (Shields)
<u>Phocides spp.</u>	Neo.	new (Brown)
<u>Sarangesa dasahara</u>	Ori.	Longstaff, 1912:391
<u>S. purendra</u>	Ori.	Longstaff, 1912:391
<u>Thorybes bathyllus</u>	Nea.	Weiss, 1927; Clark, 1936a
<u>T. confusus</u>	Nea.	Clark, 1936a
<u>T. mexicana nevada</u>	Nea.	new (many)
<u>T. pylades</u>	Nea.	Weiss, 1927; Clark, 1936a
<u>Urbanus spp.</u>	Neo.	new (Brown)
<u>Zestusa dorus</u>	Nea.	new (Scott, Shields)

Hesperiinae

<u>Abantis paradisea</u>	Eth.	Van Someren, 1955
<u>A. tettensis</u>	Eth.	Van Someren, 1955
<u>Amblyscirtes vialis</u>	Nea.	Weiss, 1927
<u>Hesperia columbia</u>	Nea.	new (Shields, Tilden)
<u>H. comma</u>	Nea.	new (Grey)
<u>H. harpalus ochracea</u>	Nea.	new (Scott)
<u>H. harpalus yosemite</u>	Nea.	new (Shields)
<u>H. juba</u>	Nea.	new (Roever, Scott)
<u>H. leonardus</u>	Nea.	new (Grey)
<u>H. metea</u>	Nea.	Clench, 1966
<u>H. miriamae</u>	Nea.	Garth and Tilden, 1963 new (Shields)
<u>H. nevada</u>	Nea.	new (many)
<u>H. pahaska</u>	Nea.	new (Scott)
<u>H. p. martini</u>	Nea.	new (MacNeill, Scott)
<u>H. p. williamsi</u>	Nea.	new (Shields)
<u>H. pawnee</u>	Nea.	new (Scott)
<u>H. sassacus</u>	Nea.	new (Grey)
<u>H. uncas</u>	Nea.	new (Scott, Shields)
<u>H. u. macswaini</u>	Nea.	new (MacNeill)
<u>H. viridis</u>	Nea.	new (Scott, Shields)

TABLE 2 (continued)

Species	Realm	Sources
<u>Polites sonora</u>	Nea.	new (MacNeill)
<u>P. themistocles</u>	Nea.	Scudder, 1887, 1889
<u>Stinga morrisoni</u>	Nea.	Tilden, 1961 new (Scott, Toliver)

Nea. = Nearctic
 Neo. = Neotropical
 Pal. = Palearctic
 Eth. = Ethiopian
 Ori. = Oriental
 Aus. = Australian

Note: many of these species are listed from various sources which mentioned in passing that a species frequented topographic prominences. Some of these may not represent hilltopping species and therefore further work to confirm or deny their validity is needed, in light of the mating-rendezvous definition of hilltopping.

eight mating pairs of Diptera on Squaw Peak, Montana. Edwards (1960) noted mating activities in summit tachinid and syrphid flies. A more detailed analysis of this mating theory will appear in the discussion section.

"Swarms" of male insects are associated with mating and are sometimes present on summits. Although Craig (1944) and Nielsen and Greve (1950) claim that certain Diptera swarms were not formed for mating, other workers have found that mating occurs when females enter male swarms in a variety of families (Knab, 1907; Gibson, 1942; Bailey, 1948; Downes, 1958; Blickle, 1959; Shemanchuk and Weintraub, 1961; Powell, 1964b; Thompson, 1967). Swarming of winged ants is also associated with mating (Wheeler, 1917b; Michener, 1948, 1960; Chapman, 1954b, 1957, 1963). In the biting Nematocera flies, the swarm develops visually to a "swarm-marker" such as a clearing or summit where both sexes respond to the marker; such swarms function to concentrate the population for the purpose of mating (Downes, 1958).

Another theory often given to explain the presence of insects on summits is that wind bears them up, particularly warm air updrafts. This idea has been mentioned for insects in general by Bowditch (1896), Guppy (1897), Rowland-Brown (in Poulton, 1904), Meinecke (1917), Bryan (1926), and Alexander (1940), and for winged ants by Wheeler (1905, 1917a) and Gregg (1947). As Chapman (1954a, 1954b, 1957) pointed out, however, updrafts may account for the presence of some but not all insects on summits (see Discussion).

Current theories to explain "hilltopping" in butterflies are reviewed by Shoumatoff (1953) and Shepard (1966). Apparently, Shepard (1966) is the only person to have made observations of more than a casual nature on hilltopping butterflies by using a mark-recapture technique. It appears that little attempt has been made in the past to apply to butterflies the findings for other summit-frequenting insects.

The different theories for the "hilltopping" of butterflies are listed in Table 3. Wind theories can be dispelled for the same reasons mentioned by Chapman (1954a) for insects (see Discussion). The presence of larval foodplants on summits can be ruled out as a theory since many hilltopping species ascend far away from the foodplant area (see, for example, Clark, 1936a; Muspratt, 1954; Emmel & Emmel, 1967) as pointed out by Knudsen (1954) and Van Someren (1955). Males "liking" hilltops as a playground, battleground, or assembly area or as a

TABLE 3. Butterfly hilltopping theories

Theory	Sources
1. Wind and/or updraft transported	Newcomer, 1910 Guppy, 1925 Merritt, 1952 Beall, 1953 Knudsen, 1954 Rawson, 1955 Shepard, 1966
2. Wind on summit as enticement	Beutenmuller, 1898 Muspratt, 1954 Emmel and Emmel, 1962
3. Unidirectional flight plus wind	Beall, 1953 Shepard, 1966
4. "Liking" hilltops (urge to ascend)	Scudder, 1863:620 Wright, 1906:86 Merritt, 1952 Shoumatoff, 1953
5. Ascend for "assembling"	Beutenmuller, 1898
6. Male surplus	Merritt, 1952
7. Male "playground" or "sporting ground"	Comstock, 1927:20, 42, 265 Clark, 1932:192 Clark, 1936a:24-25 Clark, 1936b:384, 405 Barrett and Burns, 1951:4-5, 144
8. Male "battleground"	Wright, 1906:86. 112 Rawson, 1951
9. Tropism	Merritt, 1952
10. "Phototropic urge" (attraction to warmth and light)	Van Someren, 1955
11. Foodplant on summit	Wright, 1906:112 Arnhold, 1952 Merritt, 1952 Emmel and Emmel, 1962
12. Congregation point for mating	Seitz, 1909:13, 14 Moffat, 1922 Peile, 1923:62 Clark, 1932:192 Guppy, 1962 Emmel and Emmel, 1967

response to a tropism urge does not go far in explaining the phenomenon because natural selection would eradicate this tendency for males to congregate away from females (Guppy, 1962). Surplus males congregating on summits due to the "extrovertive" male flight behavior is probably a misconception (Shepard, 1966). The idea that updrafts congregate butterflies due to the hilltop interrupting the butterfly's undirectional flight (Shepard, 1966) is inadequate because the event occurs also on still days (Knudsen, 1954) and because of the "up-and-over" tendency observed for nonhilltopping species reported here. The ideas that hilltops are meeting areas for the sexes to mate, shown to be the explanation for certain other insects, will be presented and discussed in detail in this paper as the best explanation of the phenomenon of hilltopping in butterflies.

MATERIALS AND METHODS

Observations were made continuously from March 1966 to April 1968 (except for the months of July and August), with emphasis on the winter and spring months. A total of 245 hours on 170 days was spent observing and collecting on the summit of Dictionary Hill, San Diego County, California. Some observations were made for an entire day, but most were for one to four hours, generally between midmorning and midafternoon.

Visual sightings of species in the field were recorded. Activities such as perching, feeding, chasing, courtship, mating, roosting, and predation were noted as they occurred. The occurrence and behavior of females on the summit were particularly checked to determine the validity of the summit-mating theory. Careful note was made of all species present on the summit and whether they exhibited hilltopping behavior or "up-and-over" flight. The proximity of larval foodplants of these species to the summit was checked. Flight behavior in relation to wind and updrafts was noted.

Butterflies were collected with an insect net in the air or when they alighted. All identifications were made to species. Extensive marking of male hilltopping butterflies was done to determine the habits of individuals of each species. A total of 1,011 specimens was marked. The "1-2-4-7" system (Ehrlich & Davidson, 1960) was soon found to be the best method for marking and satisfied most of the criteria for an ideal marking technique described by Gangwere et al. (1964). Eight different colored "Marks-A-Lot" felt-tip pens were used. The dye stain left on the wing was quick-drying, waterproof, and permanent without

affecting flight. Specimens could be marked quickly and recognized individually by this method. The maximum number that could be marked at one time with one color was 154. Papilionidae and Nymphalidae were held gently with wings shut between thumb and forefinger for application of the marks to the wing underside. The more delicate Pieridae, Lycaenidae, and Hesperidae were marked through the netting after being gently confined. Marked specimens were not placed in glassine envelopes except in release experiments. In most cases butterflies had to be recaptured for their numbers to be read.

Marking had no apparent injurious effect on the individual. Released specimens either alighted, flew rapidly downhill, or resumed their previous activity. Many specimens marked that initially flew downhill soon returned. "Normal" activities were seen to resume in many marked specimens. For example, often two males that were chasing each other when netted continued doing so when released. Also, males frequently returned to perch in a previous territory or "fly" area after marking. Specimens were not always released at the point of capture but were always released on the summit immediately after marking. Number, sex, wing condition, and time of capture were recorded for each marked specimen.

The *Papilio zelicaon* males used in release experiments away from the hill were netted, marked, placed in glassine envelopes, and stored in a cigar box which was kept in the shade. These experiments were carried out during periods when their population density was low so that their recapture was easier. *P. zelicaon* was used because its presence was conspicuous and it was relatively easy to recapture.

Females were collected on the summit whenever possible to check if they were mated or virgin. Male Lepidoptera deposit sperm in membranous saclike spermatophores. The bursa copulatrix of each female was later dissected under a binocular dissecting scope to check for the presence of a spermatophore (see Ouye et al., 1964; Burns, 1966; Taylor, 1967). Also, bursae from females of certain species from nonhilltop areas were dissected for comparison. A total of 548 bursae was examined during the survey: 281 from hilltop areas and 267 from nonhilltop areas. The two assumptions that Burns (1966) made are also assumed here: (1) the male transfers one spermatophore per mating, and (2) the spermatophore walls can be recognized even when collapsed. Females lacking a spermatophore were assumed to be virgin; such females were usually in fresh wing condition.

Collected females were either stored under refrigeration or their abdomens were transferred to 80 percent ethyl alcohol for later inspection. Dried females were checked from previous collections. Their abdominal tissues were reclaimed for dissection by the technique described by Van Cleve and Ross (1947), which consists of soaking the abdomens for 24 to 72 hours in a solution of trisodium phosphate diluted to 0.5 percent with distilled water.

Weather readings were taken when *in copula* pairs were observed and at the time that hilltoppers first arrived for the day. Air temperature, relative humidity, and wind velocity were recorded on the summit by taking head-high readings with a Dwyer anemometer and a Bacharach sling psychrometer. Pacific Standard Time was used throughout the study.

For comparative purposes, certain other summits in San Diego County were occasionally visited to mark and observe hilltopping species. These included a hill 997 feet in elevation, 1.7 miles south-southeast of the El Cajon Post Office; a hill 842 feet high 0.9 miles east of Dictionary Hill; Cowles Mountain; Tecate Mountain; Monument Peak; Mount Kentwood; and "Two Mile Hill," one mile west of Scissors Crossing, 6.5 air miles east of Julian.

Location and Description of Study Area

Dictionary Hill is 1,064 feet in elevation and is located one mile south of Spring Valley and 1.75 mile north of Sweetwater Reservoir (T. 17 S., R. 1 W., Sects. 5, 32, 33), San Diego County, California (Fig. 1). The nearest higher hills are Mount Helix (1,373 feet), 2.9 air miles to the north-northeast; Mother Miguel Mountain (1,527 feet), 3.3 air miles to the south-southeast; and San Miguel Mountain (2,565 feet), 3.9 air miles to the southeast. Three lesser knobs on the eastern slopes of Dictionary Hill are 924 feet, 842 feet, and 677 feet high. The surrounding lowlands range from 200 to 800 feet below the summit of the hill.

The hill consists of Jurassic-Triassic meta-volcanic rocks, with a rough stony land soil-type. The climate of the area is dry summer Mediterranean. La Mesa, California, at 560 feet, located three miles to the north of Dictionary Hill, has the following climatic features: the average maximum temperature is 75.0° F, the average minimum temperature is 50.0° F, the average mean temperature is 62.5° F, the average number of days with 0.01 inches or more precipitation is 44, and the average growing season is 327 days (Felton, 1965).



Fig. 1. Dictionary Hill (A) and Hill 842 (B), as seen from the southeast.

The plant community on the slopes of Dictionary Hill is Coastal Sage Scrub, according to the classification of Munz and Keck (1965). Indicator plants present include California Sagebrush (*Artemisia californica*), California Buckwheat (*Eriogonum fasciculatum*), Golden Yarrow (*Eriophyllum confertiflorum*), White Sage (*Salvia apiana*), and Black Sage (*S. mellifera*). Four conspicuous shrubs present are Broom Baccharis (*Baccharis sarothroides*), Monkey-flower (*Mimulus puniceus*), Redberry (*Rhamnus crocea*), and Laurel Sumac (*Rhus laurina*). Other plants on the slopes include Locoweed (*Astragalus* sp.), Slender Wild Oat (*Avena barbata*), Black Mustard (*Brassica nigra*), Blue Dicks (*Brodiaea pulchella*), White Forget-me-not (*Cryptantha intermedia*), Dodder (*Cuscuta* sp.), Tansy-Mustard (*Descurainia* sp.), Sweet Fennel (*Foeniculum vulgare*), certain grasses, Deerweed (*Lotus scoparius*), Plantain (*Plantago Hookeriana* var. *californica*), Figwort (*Scrophularia californica*), Wild Pansey (*Viola pedunculata*), and others.

The summit of Dictionary Hill was graded at one time and presents an elliptically shaped flat area measuring about 230 by 275 feet (Fig. 2). This area is covered by Broom Baccharis. Most of the observations were made near sumac clumps at the northeast and southwest edges, where hilltopping activity was most intense.

In the fall of 1958 a fire destroyed the vegetation on the western slope of Dictionary Hill. The area has since grown back considerably, but the fire probably destroyed a colony of *Chlosyne leanira wrightii*, a species that was common on the summit from 1955-1958. Three males were collected there on April 3, 1960, but none have been taken since that time. Its foodplant, *Castilleja* sp., grew on the west slope. *C. l. wrightii* specimens used to fly in areas where *Papilio zelicaon* and *Euphydryas chalcedona* hilltopped on the summit (Breedlove, personal communication). Thus *C. l. wrightii* may have been another hilltopping species.

RESULTS

Species Present

Forty-five species of butterflies were collected on the summit of Dictionary Hill during 1966-1968. A forty-sixth species, *Chlosyne leanira wrightii*, has not been collected there since 1960 (Table 4 and Fig. 3 and 4). Twenty-one of these were considered as hilltoppers because of their territorial or patrol behavior of males confined to the summit, as opposed to the twenty-five non-hilltopping species that flew "up-and-over," fed without remaining, or did not congregate at the summit (Table



Fig. 2. Dictionary Hill summit with Broom Baccharis.

TABLE 4. Summit of Dictionary Hill, Spring Valley
San Diego County, California. Species present
collected by Oakley Shields

Hilltoppers	Non-hilltoppers
PAPILIONIDAE	PIERIDAE
<u>Battus philenor</u>	<u>Anthocaris sara</u>
<u>Papilio eurymedon</u>	<u>Colias eurytheme</u>
<u>Papilio zelicaon</u>	<u>Colias harfordii</u>
	<u>Zerene cesonia</u>
PIERIDAE	<u>Eurema nicippe</u>
<u>Anthocaris cethura</u>	<u>Phoebis sennae</u>
<u>Pieris protodice</u>	+ <u>Pieris rapae</u>
	NYMPHALIDAE
NYMPHALIDAE	<u>Agraulis vanillae</u>
<u>Chlosyne leanira</u>	<u>Chlosyne gabbi</u>
<u>wrightii</u>	<u>Coenonympha tullia</u>
<u>Euphydryas editha</u>	<u>californica</u>
<u>Euphydryas chalcedona</u>	<u>Danaus plexippus</u>
<u>Speyeria callippe</u>	<u>Danaus gilippus berenice</u>
<u>comstocki</u>	<u>Junonia coenia</u>
<u>Vanessa atalanta</u>	<u>Nymphalis antiopa</u>
<u>Vanessa cardui</u>	
<u>Vanessa caryae</u>	LYCAENIDAE
<u>Vanessa virginiensis</u>	* <u>Apodemia mormo virgulti</u>
	<u>Brephidium exilis</u>
LYCAENIDAE	+ <u>Everes comyntas</u>
<u>Atlides halesus</u>	<u>Glaucopsyche lygdamus</u>
<u>Callophrys dumetorum</u>	<u>australis</u>
<u>Celastrina argiolus</u>	<u>Lycaena helloides</u>
<u>echo</u>	* <u>Philotes battoides bernardino</u>
<u>Incisalia iroides</u>	
<u>Leptotes marina</u>	HESPERIIDAE
<u>Satyrrium saepium</u>	<u>Erynnis funeralis</u>
<u>Strymon melinus</u>	<u>Heliopetes ericetorum</u>
	<u>Hylephila phyleus</u>
HESPERIIDAE	* <u>Ochlodes sylvanoides</u>
<u>Erynnis tristis</u>	<u>Pyrgus communis</u>

Total number of species = 46

0/0 of total that are hilltoppers = 45.7

+ = reported in the literature as hilltopping

* = species that rarely showed a territorial or aggressive activity but did not concentrate on the summit

5). Of these non-hilltopping species persent, both *Apodemia mormo virgulti* and *Everes comyntas* remained on and near the summit and one *in copula* pair was observed at the summit for both. However, these species were not particularly concentrated at the summit and occurred in about equal numbers on the slopes of Dictionary Hill as well. During 1960 K. Roever found 28 butterfly species on "A" Mountain summit, Tucson, Arizona (Table 6). The proportion of hilltopping species to non-hilltopping species at "A" Mountain and Dictionary Hill was remarkably similar (46% at both locations were hilltopping species).

Certain species were present in the canyon bottoms to the east, southeast, and south of Dictionary Hill (2,000-5,000 feet away from the summit) that were not collected on the summit: *Pieris beckerii*, *Philotes sonorensis*, *Poanes melane*, and *Urbanus proteus* (one). All but the last named were regular residents of the canyon bottoms, along with the non-hilltopping species *Anthocaris sara*, *Nymphalis antiopa*, *Junonia coenia*, and *Chlosyne gabbii* that were occasionally present on the summit.

Territorial and Aggressive Behavior

Most of the specimens that showed hilltopping behavior were males. This fact was determined by visual observation and capture of the 21 hilltopping species. In those species where the sexes were difficult to determine visually (e.g., *Vanessa* and *Erynnis*), captured specimens were nearly always males.

All of the hilltopping males except two pierid species established perch sites (*P. protodice* and *A. cethura* milled about without landing except occasionally to feed). The preferred perch site of *V. atalanta*, *V. cardui*, *V. carye*, and *C. dumetorum* was the ground or vegetation close to the ground. *V. atalanta* seemed especially partial to perching on rocks in clearings (Fig. 5). *V. virginensis* was the only *Vanessa* species to consistently perch off the ground on vegetation (one to three feet up), although the others did so sometimes. Other species that perched on vegetation well above ground were *B. philenor*, *P. eurymedon*, *P. zelicaon* (Fig. 6) (on the ground occasionally), *A. halesus*, *S. melinus* (Fig. 7), *S. saepium*, *C. a. echo*, and *E. tristis* (Fig. 8). *E. chalcedona* perched on the ground, ground vegetation, and rocks in clearings and sometimes on vegetation one to two feet up. *B. philenor* and *P. eurymedon* rarely alighted and flew almost continuously in milling over the summit. Once landed, perched species usually faced perpendicular to the sun's rays.

The pattern of establishing and returning to perch sites was noted. *P. zelicaon* flew back and forth over an area and alighted



Fig. 3. Species of hilltopping butterflies from the summit of Dictionary Hill, males only: (1) *Battus philenor*, (2) *Papilio eurymedon*, (3) *Papilio zelicaon*, (4) *Anthracaris cethura*, (5) *Pieris protodice*, (6) *Chlosyne leanira* wrightii, (7) *Euphydryas editha*, (8) *Euphydryas chalcedona*, (9) *Speyeria callippe comstocki*, (10) *Vanessa atalanta*, (11) *Vanessa cardui*, (12) *Vanessa caryae*, (13) *Vanessa virginiensis*, (14) *Atides halesus*, (15) *Callophrys dumetorum*, (16) *Celastrina argiolus echo*, (17) *Incisalia iroides*, (18) *Leptotes marina*, (19) *Saturium saepium*, (20) *Strymon melinus*, (21) *Erynnis tristis*.



Fig. 4. Species of non-hilltopping butterflies from the summit of Dictionary Hill, males only: (1) *Anthracaris sara*, (2) *Colias eurytheme*, (3) *Colias harfordii*, (4) *Zerene cesonia*, (5) *Eurema nicippe*, (6) *Pieris rapae*, (7) *Phoebis sennae*, (8) *Danaus plexippus*, (9) *Danaus gilippus berenice*, (10) *Coenonympha tullia californica*, (11) *Agraulis vanillae*, (12) *Chlosyne gabbii*, (13) *Junonia coenia*, (14) *Nymphalis antiopa*, (15) *Apodemia mormo virgulti*, (16) *Brephidium exilis*, (17) *Everes comyntas*, (18) *Glaucopsyche lygdamus australis*, (19) *Lycaena helloides*, (20) *Philotes battoides bernardino*, (21) *Erynnis funealis*, (22) *Heliopterus erictorum*, (23) *Hylephila phyleus*, (24) *Ochlodes sylvanoides*, (25) *Pyrgus communis*.

TABLE 5. Non-hilltoppers present on the summit of Dictionary Hill during 1966-1968

Species	Comments
1. <u>Anthocaris sara</u>	Both sexes flying over, mostly females, occasional oviposition behavior.
2. <u>Colias eurytheme</u>	Both sexes flying over.
3. <u>Colias harfordii</u>	One male flying over.
4. <u>Zerene cesonia</u>	One male flying over.
5. <u>Eurema nicippe</u>	Some seen flying over, one female collected.
6. <u>Pieris rapae</u>	Both sexes flying and feeding.
7. <u>Phoebis sennae</u>	Two males flying over.
8. <u>Danaus gilippus berenice</u>	One male flying over.
9. <u>Danaus plexippus</u>	Several seen flying over.
10. <u>Coenonympha tullia californica</u>	A few males flying over.
11. <u>Agraulis vanillae</u>	Two males collected, other specimens seen flying over.
12. <u>Chlosyne gabbi</u>	Male and female collected.
13. <u>Junonia coenia</u>	A few seen flying over.
14. <u>Nymphalis antiopa</u>	A number seen flying over, Two males territorial.
15. <u>Apodemia mormo virgulti</u>	Both sexes present in numbers on summit but no concentrations; two in copula pairs collected near summit.
16. <u>Brephidium exilis</u>	Male and female feeding.
17. <u>Everes comyntas</u>	Males and females flying near summit, one in copula pair collected near summit.
18. <u>Glaucopsyche lygdamus australis</u>	Males flying over, females occasionally present.
19. <u>Lycaena helliodes</u>	A female feeding.
20. <u>Philotes battoides bernardino</u>	Two males territorial.
21. <u>Erynnis funeralis</u>	A number seen, several males and a female collected flying over and feeding.
22. <u>Heliopetes ericetorum</u>	Several males flying over, one male collected.
23. <u>Hylephila phyleus</u>	One male feeding.
24. <u>Ochlodes sylvanoides</u>	Two males territorial.
25. <u>Pyrgus communis</u>	Occasional specimens flying over.

+ Not enough present to say if males preferred the summit or not.

TABLE 6. Summit of "A" Mountain, West of Tucson,
Pima County, Arizona. Species present during
1960, collected by Kilian Roever

Hilltoppers	Non-hilltoppers
PAPILIONIDAE	PIERIDAE
<u>Battus philenor</u>	<u>Anthocaris sara</u>
<u>Papilio polyxenes</u>	<u>Colias eurytheme</u>
<u>asterius</u>	<u>Eurema nicippe</u>
<u>Papilio rudkini</u>	<u>Nathalis iole</u>
	<u>Phoebis sennae</u>
PIERIDAE	<u>Zerene cesonia</u>
<u>Anthocaris pima</u>	NYMPHALIDAE
<u>Euchloe hyantis lotta</u>	<u>Agraulis vanillae</u>
<u>Pieris protodice</u>	<u>Asterocampa leilia</u>
NYMPHALIDAE	<u>Chlosyne lacinia</u>
<u>Vanessa atalanta</u>	<u>Danaus gilippus strigosus</u>
<u>Vanessa cardui</u>	<u>Danaus plexippus</u>
<u>Vanessa caryae</u>	LIBYTHEIDAE
<u>Vanessa virginiensis</u>	<u>Libytheana bachmanii</u>
LYCAENIDAE	LYCAENIDAE
<u>Atlides halesus</u>	+ <u>Leptotes marina</u>
<u>Strymon melinus</u>	HESPERIIDAE
HESPERIIDAE	<u>Erynnis funeralis</u>
<u>Hesperia pahaska</u>	<u>Pyrgus communis</u>
<u>williamsi</u>	

Total number of species = 28

0/0 of total that are hilltoppers = 46.4

+ = reported in this paper as hilltopping.

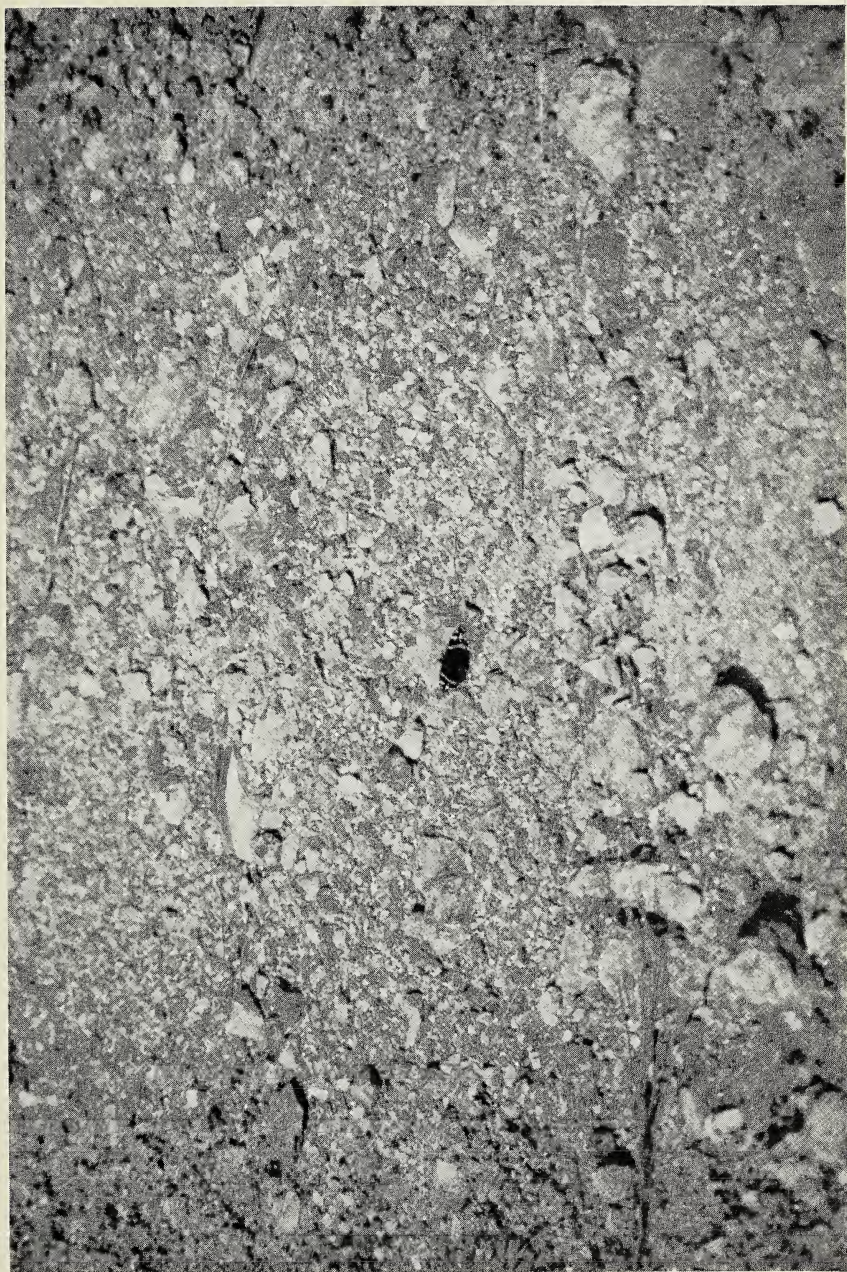


Fig. 5. Male *Vanessa atalanta* in perched position.



Fig. 6. Male *Papilio zelicaon* in perched position.



Fig. 7. Male *Strymon melinus* in perched position.



Fig. 8. Male *Erynnis tristis* in perched position.

on plants within the same area after leaving the first perch in chases. Three *P. eurymedon* observed on different days flew lazily about the northeast side of the summit for about ten minutes before landing on the same sumac bush. *E. chalcidona* usually perched at various places in a particular clearing after each chase from a perch. All the *Vanessa* species seemed indifferent about where they would perch. They were not drawn to a particular spot or clearing and readily established a new perch area after a chase. All of the three *A. halesus* males perched on a particular sumac on the northeast top.

From these perch sites, investigative flights directed at the same species, different species, and sometimes different insects were taken. When an individual of the same species passed a perched male, the perched male flew up to investigate, gave pursuit, and frequently engaged in a "battle" with the other male. Perched *P. zelicaon* males rapidly pursued passing *P. zelicaon* for considerable distances before breaking away and returning to the vicinity of the perch. Sometimes three or four *P. zelicaon* pursued in a chain. Frequently two *P. zelicaon* males would engage in a "battle," especially when males first established their territories during the morning. They flew in tight circles around each other and climbed high into the air, sometimes locking legs and audibly beating wings. (Eff [1962] has observed that *Papilio indra minori* males may physically damage each other in such encounters by beating their wings and falling to the ground while their legs are locked together.) *E. chalcidona*, *S. melinus*, and *C. dumetorum* were often seen to spin about each other in these high, climbing flights before breaking away and returning to the perch area. When two males of a *Vanessa* species met, they climbed at a slight angle to the ground, usually into the wind, with the pursuer behind the pursued. In all cases where identity could be determined by identifiable wing defects or marked specimens, it was the original male that returned after leaving the perch in the territorial species. This is what has been observed with territorial males in *Hesperia* (MacNeill, 1964), *Hesperia metea* (Shapiro, 1965), *Agathymus evansi* (Roever, 1964), and in hundreds of instances in the bot fly *Cuterebra latifrons* on hilltops (Catts, 1963).

Investigative flights by milling pierids were noted. Typically when two *A. cethura* met, one chased the other, with the pursuer often becoming the pursued. Frequently other *A. cethura* and sometimes a *P. protodice* would join. Up to eight *A. cethura* were seen in such a "cloud." The two pierid species usually

followed a stereotyped, predictable pathway in approaching and flying on the summit. Marked *P. protodice* and *A. cethura* did not remain on the summit for long periods but were recaptured at intervals during the morning and early afternoon on the summit along their patrol pathways.

Investigative and chase flights against different species by perched and patrolling males frequently occurred, but inter-specific battles were rarely seen. Often the other species was considerably smaller or larger or had a different color or different flight pattern. Table 7 lists some of the species that hilltopping species pursued. Investigative and chase flights of other orders of insects were noted for *P. zelicaon* (black dragonfly), *V. atalanta* (red dragonfly), *E. chalcidona* (black reduviid and black syrphid), *S. melinus* (flies, red dragonfly and yellow wasp), and *E. tristis* (flies).

The behavior of a particular *S. melinus* male with chipped wings was observed in detail for 55 minutes on October 23, 1966. The entire time he perched on a sumac bush with wings half open and did not fly except to investigate flying insects. One continuous sitting period lasted 14 minutes. He was twice seen to pass the forelegs over the eyes and antennae while twisting the head, much as flies do when "cleaning." This same individual was noted to return after one elapsed day to the same sumac bush to perch. On following days his perch area was occupied by other *S. melinus* males.

Daily Residence

Various males of hilltopping species remained on the summit for long periods of time during the day (* = undisturbed arrival and departure observed):

Species	No.	Time in continuous residence on summit (min.)
<i>Battus philenor</i>	1	70
<i>Papilio eurymedon</i> *	1	37
<i>P. zelicaon</i>	1	110
<i>Atlides halesus</i> *	1	82
<i>Callophrys dumetorum</i>	1	91
<i>Strymon melinus</i>	2	30, 55
<i>Celastrina argiolus echo</i>	1	116

Most males recaptured more than once on the same day were not observed continuously. Maximum times between when first and last collected on the summit during the day for these were:

TABLE 7. Investigative and/or pursuit flights
observed among different butterfly
species on Dictionary Hill

(Pursuer species listed first)

<u>P. zelicaon</u>	<u>V. caryae</u>
<u>P. eurymedon</u>	<u>P. zelicaon</u>
<u>A. cethura</u>	<u>P. protodice</u>
<u>E. chalcedona</u>	<u>C. tullia</u>
<u>V. caryae</u>	<u>V. virginiensis</u>
<u>E. tristis</u>	<u>E. tristis</u>
<u>A. cethura</u>	<u>S. melinus</u>
<u>P. zelicaon</u>	<u>N. antiopa</u>
<u>P. protodice</u>	<u>V. cardui</u>
<u>A. sara</u>	<u>V. virginiensis</u>
<u>C. tullia</u>	<u>P. b. bernardino</u>
	<u>E. tristis</u>
<u>P. protodice</u>	<u>S. saepium</u>
<u>P. rapae</u>	<u>V. virginiensis</u>
<u>A. cethura</u>	
<u>E. chalcedona</u>	<u>C. dumetorum</u>
<u>P. zelicaon</u>	<u>E. chalcedona</u>
<u>V. atalanta</u>	<u>Vanessa sp.</u>
<u>V. atalanta</u>	<u>E. tristis</u>
<u>V. cardui</u>	<u>V. caryae</u>
<u>V. caryae</u>	
<u>V. virginiensis</u>	
<u>V. virginiensis</u>	
<u>P. zelicaon</u>	
<u>V. atalanta</u>	
<u>V. caryae</u>	
<u>S. melinus</u>	

Species	Elapsed time (min.)
<i>Anthocaris cethura</i>	213
<i>Pieris protodice</i>	140
<i>Speyeria callippe comstocki</i>	150
<i>Vanessa atalanta</i>	123
<i>V. cardui</i>	12
<i>V. caryae</i>	87
<i>V. virginiensis</i>	82
<i>Leptotes marina</i>	25
<i>Erynnis tristis</i>	45

An attempt was made on May 16, 1966, to recapture *Euphydryas chalcedona* males in the afternoon that were marked in the morning. *E. chalcedona* were marked and recaptured during two 80-minute periods, from 0800-0920 and from 1223-1343 hours. Thirty-one individuals were marked, 19 in the morning and 12 in the afternoon. Only about 10 individuals were seen that were not marked. Five specimens were recaptured: after 15, 44, 50, 246, and 318 elapsed minutes. Only two from the morning period were recaptured in the afternoon. The data suggest that there was a high rate of turnover during the course of the day.

One marked *P. zelicaon* male was seen in territorial behavior on the summit on eight different days over a 20-day period (December 19, 1966, to January 8, 1967). This male frequented a particular area on the south side of the summit from which it "attacked" other male *zelicaon* in battles and pursuit flights. Fig. 9 is a summary of the times during the day it was observed.

Numbers of specimens recaptured at different times on a given day (after at least ten minutes of elapsed time) on summits during this study are as follows:

<i>Battus philenor</i>	1
<i>Papilio eurymedon</i>	13
<i>P. indra pergamus</i>	3
<i>P. rudkini</i>	5
<i>P. zelicaon</i>	66
<i>Anthocaris cethura</i>	29
<i>Pieris protodice</i>	13
<i>P. sisymbrii</i>	4
<i>Euphydryas chalcedona</i>	13
<i>Speyeria callippe comstocki</i>	3
<i>Vanessa atalanta</i>	7
<i>V. cardui</i>	2
<i>V. caryae</i>	1

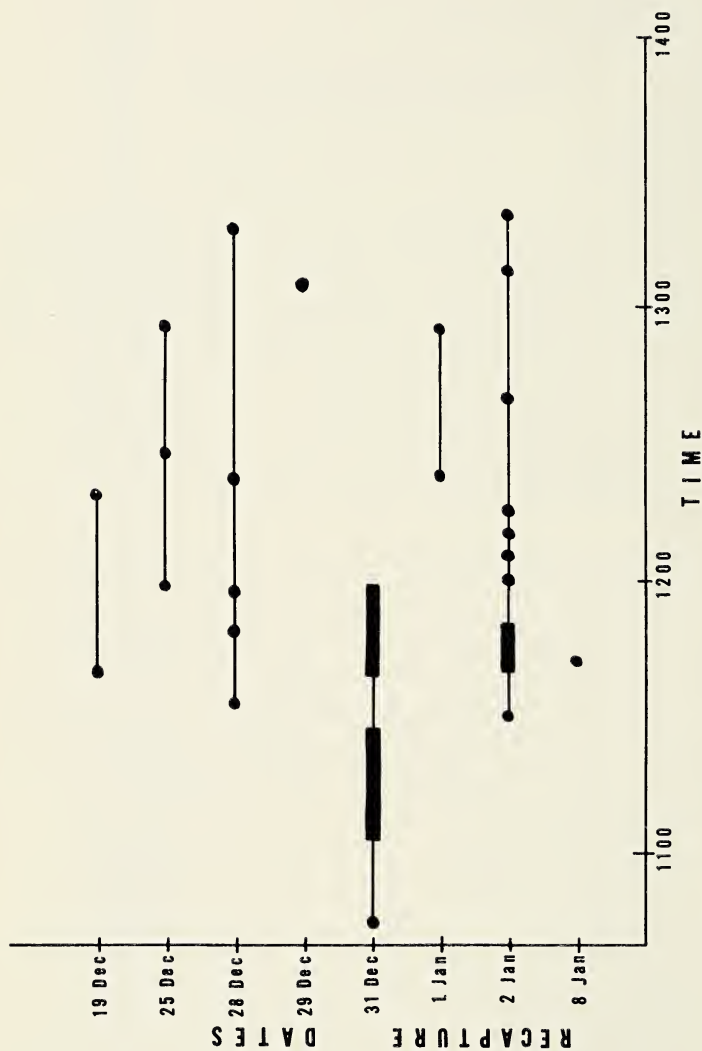


Fig. 9. Summary of times when a marked male *Papilio zelicaon* was observed over a 20-day period on Dictionary Hill summit. Dots represent individual recaptures and bars represent periods when continuously seen.

<i>V. virginiensis</i>	5
<i>Atlides halesus</i>	3
<i>Callophrys dumetorum</i>	9
<i>Celastrina argiolus echo</i>	8
<i>Leptotes marina</i>	1
<i>Strymon melinus</i>	3
<i>Erynnis tristis</i>	2

These numbers indicate that at least a substantial number of hilltopping males remain for periods of time on a summit on a given day.

Daily arrival as reflected by continuous collecting on a summit on a given day was determined for *Papilio zelicaon*, *P. eury-medon*, and *Anthocaris pima* (Table 8). In each case a majority arrived within the first hour after the first individual for the day had arrived, with the remainder arriving two to two-and-one-half hours after the first hour.

Diurnal Periodicity

Initial sightings of males in hilltopping activity were observed for the four *Vanessa* species. These first flew to the summit to hilltop only in the afternoons between 1220 and 1515 hours. Generally all four species were present on a given day. On six days, two to three of the species initially hilltopped together. The first species to be sighted in hilltopping behavior varied from day to day:

First species	No. days
<i>V. atalanta</i>	19
<i>V. virginiensis</i>	15
<i>V. cardui</i>	12
<i>V. caryae</i>	11

Only the first *Vanessa* of the day to remain on the summit in circling, aggression, and alighting behavior was recorded; those individuals feeding or flying over the summit were not considered.

For these *Vanessa* males, time of initial sighting, ambient air temperature, and relative humidity were recorded on 51 days during various times of the year. The time of initial sighting is correlated with air temperature and relative humidity (Fig. 10). The warmer the air temperature, the later they will arrive; the cooler it is, the earlier they will arrive. If the temperature remains constant, they would arrive earlier with decreasing relative humidity and later with increasing relative humidity. No correlations were apparent when relative humidity was plot-

TABLE 8. Daily arrival reflected by continuous collecting of butterfly species on a summit

Species, place, date	Total males	1000-1030	1030-1100	1100-1130	1130-1200	1200-1230	1230-1300	1300-1330	1330-1400	1400-1430
<u>Papilio zelicaon</u> <u>Dictionary Hill,</u> California February 4, 1967	20	0	11	3	1	2	0	3	-	-
<u>Papilio zelicaon</u> <u>Dictionary Hill,</u> California February 12, 1967	28	0	7	6	3	2	3	5	2	-
<u>Papilio eurymedon</u> <u>Tecate Mountain,</u> California April 9, 1967	23	9	3	3	3	3	0	2	-	-
* <u>Anthocaris pima</u> <u>"A" Mountain,</u> Arizona March 2, 1960	96	0	0	15	35	27	6	11	2	0

*Collected by K. Roever.

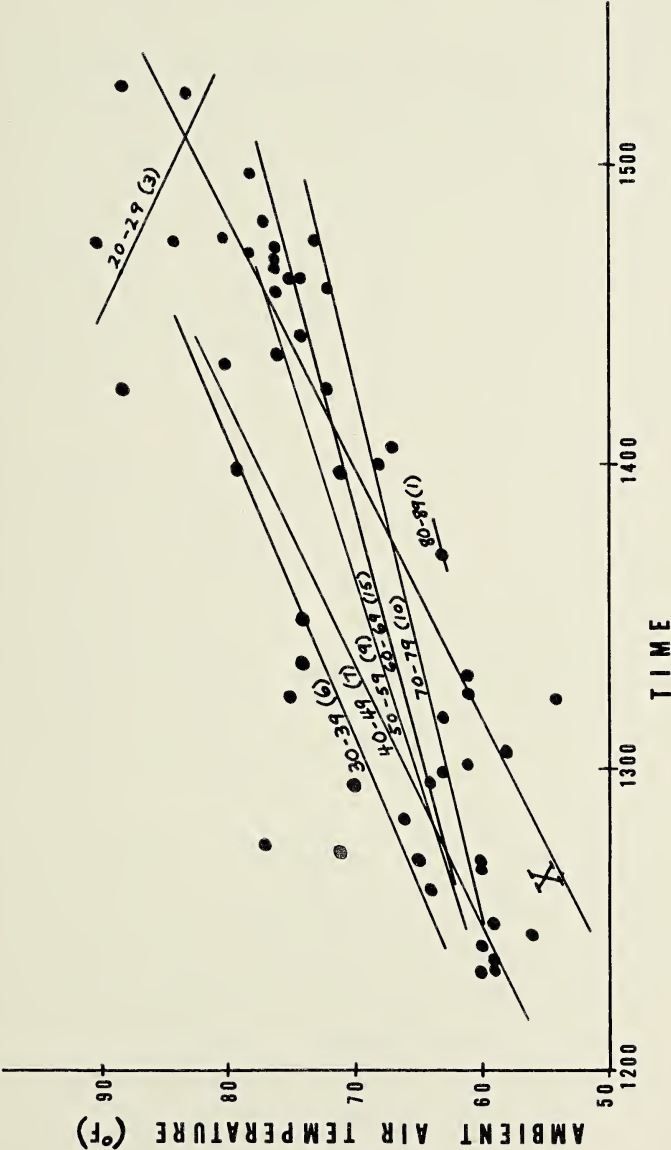


Fig. 10. Initial sightings of hilltopping *Vanessa* species. Linear regression lines by least squares are computed for a relative humidity in 10% intervals. Line "X" is the mean of all points. Time is adjusted to local apparent noon.

ted against time and when air temperature was plotted against relative humidity. Wind velocity, amount of overcast, and barometric pressure were not considered but may also be influencing factors.

Migration

Butterfly migrations have occasionally been reported to pass over summits of hills and mountains. Species reported include *Vanessa cardui* (Fritsch, 1879; Wright, 1906:37), *Danaus plexippus* (Edwards and Scudder, 1877), and a *Delias* species (Poulton, 1921, 1922). In these instances no "staying" behavior at the hilltop was shown by the migrants. A migration of *V. cardui* to the north on Dictionary Hill on March 30, 1966, behaved much as Wright (1906:37) described. Specimens flew upslope from the south, flew across the summit, and kept flying up and out off the north slope instead of proceeding downhill. Other individuals were noted to pass over the hill's shoulders. No concentration toward the summit by the flight was noted.

Mark-Recapture Study

Fourteen hilltopping species comprising 968 males were marked on Dictionary Hill summit. The percentage of recaptures after one elapsed day for these species varied from 0 to 38 percent with a mean of 13.5 percent (Table 9). For comparison with another hilltop, six hilltopping species were marked and recaptured on Two Mile Hill in a desert environment (Table 10). On Dictionary Hill, *P. zelicaon*, *A. cethura*, and *C. dume-torum* had the highest percentages of recapture and the four *Vanessa* species had the lowest. The low rate of recapture for *Vanessa* species was probably due to the difficulty of capturing these and the large numbers of individuals of *Vanessa* present on any one day.

Catts (1963) found that resightings of marked males of the hilltopping bot fly *Cuterebra latifrons* on a hilltop was 25.7, 29.5, and 33.3 percent over a three-year period. Apparently no mark-recapture work with hilltopping butterflies has been done besides Shepard's work (1966) with *Pieris occidentalis*. Results of marking butterflies from non-hilltop areas are summarized in Table 11.

The elapsed days from marking to recapture for eight species on Dictionary Hill summit are summarized in Table 12. It is evident that these species often return to the summit after a number of days have passed. There is some evidence that certain males may spend their entire life on the summit, judging from certain individuals that had fresh wing condition when

TABLE 9. Mark-recapture results for male butterflies on Dictionary Hill summit (on 95 different days)

Species	Number marked	Number recaptured	0/0 Recaptured after one/more elapsed days	Longest no. days to recapture
<u>Papilio zelicaon</u>	389	126	32.4	29
<u>Papilio eurymedon</u>	11	1	9.1	1
<u>Anthocaris cethura</u>	64	17	26.6	14
<u>Pieris protodice</u>	66	10	15.2	6
<u>Euphydryas chalcedona</u>	144	22	15.3	10
<u>Speyeria callippe comstocki</u>	31	4	12.9	17
<u>Vanessa atalanta</u>	53	2	3.8	3
<u>Vanessa cardui</u>	46	0	0.0	-
<u>Vanessa caryae</u>	47	1	2.1	2
<u>Vanessa virginiensis</u>	18	1	5.6	1
<u>Callophrys dumetorum</u>	24	9	37.5	18
<u>Strymon melinus</u>	37	3	8.1	4
<u>Celastrina argiolus echo</u>	11	1	9.1	8
<u>Erynnis tristis</u>	27	3	11.1	4
	968	200		

*This compares well with Shepard's (1966) findings on Slate Peak, Washington, for closely related species:

<u>Pieris occidentalis</u>	41	6	14.6	14
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TABLE 10. Mark-recapture results for male butterflies on
Two Mile Hill summit, Scissors Crossing, San Diego
County, California (on three different days)

Species	Number marked	Number recaptured	0/0 Recaptured after one/more elapsed days
<u>Papilio rudkini</u>	15	4	26.7
<u>Anthocaris cethura</u>	8	5	62.5
<u>Pieris protodice</u>	2	0	*
<u>Pieris sisymbrii</u>	15	1	6.7
<u>Callophrys dumetorum</u>	2	1	*
<u>Atides halesus</u>	1 43	1 12	*

* Insignificant amount to compute percent.

TABLE 11. Mark-recapture results from other sources for butterfly species

Species	Number marked	Number recaptured	0/0 Recaptured		Habitat	Source
			after at least one day	Feeding area		
<u>Papilio glaucus</u>	49 (46m, 3f)	17	34.7			Fales, 1959
<u>Parnassius phoebus</u>	--	--	60.0	--		Shepard, 1966
<u>Anthocaris sara</u>	68 (males)	17	25.0	Canyon bottom		Evans, 1955
<u>Euchloe ausonides</u>	--	--	10.0	--		Shepard, 1966
<u>Maniola jurtina</u>	1565 * *	183	11.7	Meadows		Dowdeswell, Fisher, and Ford, 1949
<u>Erebia epipsodea</u>	--	--	25.0	Meadows		Shepard, 1966
<u>Euphydryas editha</u>	185 (mostly males)	97	52.4	Sedentary around foodplant		Ehrlich, 1961
<u>Hamadryas guatemalena</u>	9 (7m, 2f)	2	22.2	On tree trunks		Ross, 1963
<u>Vanessa atalanta</u>	67 (prob. males)	8	11.9	In garden		Fletcher, 1936
<u>Vanessa cardui</u>	7	1	14.3	In garden		Fletcher, 1936
<u>Piebejus icarioides</u>	--	--	33.0	Around foodplant		Shepard, 1966
<u>Polyommatus icarus</u>	330	86	26.1 (minimum value)	On small island		Dowdeswell, Fisher, and Ford, 1940
<u>Catocala (moths), 16 species</u>	314	30	9.1	On tree trunks		Brower, 1930

* * Sexes not differentiated

Dashes represent unknown.

TABLE 12. Elapsed days from marking to recapture for certain hilltopping species on Dictionary Hill, including separate entries for specimens taken on two or more different days.

Number days	<u>P. z. zelacon</u>	<u>A. c. cethura</u>	<u>P. p. protodice</u>	<u>E. c. chalcedona</u>	<u>S. s. callippe</u>	<u>C. d. dumetorum</u>	<u>S. s. melinus</u>	<u>E. t. tristis</u>
1	38	1	6	6	1	3	1	1
2	18	5		6			1	2
3	13	5	3	5			3	
4	16	2	1	3	1	1	1	1
5	15	2		2		2		
6	4		1					
7	22	1		3	2	2		
8	16	2		4		1		
9	8	1			2	2		
10	8			1				
11	1							
12	3							
13	7					1		
14	5	1						
15	4							
16	1				1			
17					1			
18	1					1		
19	3							
20	2							
21-26 (none)								
27	1							
28	2							
29	1							
total specimens recaptured	126	17	10	22	4	9	3	3
no. taken > once	35	3	1	6	2	4	2	1
0/0 of recaptures taken > once	27.8	17.6	10.0	27.3	*	44.4	*	*

* = entry not very significant.

first marked and had extremely worn wing condition and weak flight when finally recaptured.

Papilio zelicaon Release Experiments

One hundred and forty-three male *P. zelicaon* collected on the summit of Dictionary Hill were marked and released at various distances and degrees of the compass to see if they would "home in" on the summit (see Table 13 and Fig. 11). One-third did return, about the same percentage that were marked on the summit and were recaptured there. In one instance two males that returned from the north also returned to the summit when released from the south. One male that was released nearly three miles away flew into a wind to return.

P. zelicaon released far away from the summit homed in on a nearby hilltop. Ten male *P. zelicaon* and one male *P. eurymedon* collected on the summit of Dictionary Hill were transported four miles to the northeast and released. Two of the *P. zelicaon* and the *P. eurymedon* homed in on the summit of a hill 997 feet high 3,400 feet to the southeast of the release point. Three of 19 *P. zelicaon* males transported to the desert about 40 air miles away hilltopped on "Two Mile Hill" about one mile to the northwest of the release point.

There is some evidence that *P. zelicaon* males will return to their own hill when given a choice of hills. Two groups of males, one group from the summit of Dictionary Hill and the other from the summit of a hill 924 feet high and 2,200 feet southeast of the summit of Dictionary Hill, were released together at location number 12 (Fig. 11):

Date released	No. released	No. recapt.	Elapsed days to recapture
III-19-67	6 (from Dictionary)	4	1, 1, 1, 6
	5 (from 924')	1	1
IX-27-67	4 (from Dictionary)	3	1, 1, 1
	1 (from 924')	1	1

On both dates all the recaptures were from the hilltop where the specimen was originally collected. The specimen collected on Hill 924 on September 28, 1967, was released on the summit of Dictionary Hill and returned the next day to the summit of Hill 924.

Minimum speed of return to the summit of Dictionary Hill was estimated for four *P. zelicaon* males that were recaptured on the same day:

TABLE 13. Marked male *Papilio zelicaon* recaptured on top of Dictionary Hill after release away from the summit (see Fig. 12)

No. of location	Distance from summit (ft)		Date released	Number released	Number recaptured	Elapsed days to recapture
	Vertical	Horizontal				
1	765	7,200	I-14-67	13	5	1,1,1,1,12
2	640	5,500	II-5-67	5	2	6,7
3	595	14,000	II-11-67	11	1	1
4	715	6,400	I-8-67	6	4	1,1,1,1
5	715	7,900	II-4-67	10	2	1,18
6	685	4,000	I-29-67	5	2	4,6
9	365	5,000	II-2-67	4	3	2,2,2
10	285	4,400	II-4-67	10	1	1
11	205	1,200	III-2-67	1	1	5
12	265	2,600	I-7-67	5	4	1,1,2,2
			I-9-67	7	1	1
			II-13-67	27	7	0,0,0,3,7,9,27
			II-28-67	2	1	7
			III-12-67	3	0	-
			III-16-67	2	0	-
			III-19-67	6	4	1,1,1,6
			III-20-67	10	2	5,5
			IX-27-67	4	3	1,1,1
13	365	1,800	II-16-67	5	4	4,4,4,10
14	665	7,600	XII-24-67	2	0	-
			XII-26-67	5	1	0
				143	48	
				recapture = 33.6 0/0		

Specimens released at locations 7, 8, and 9 were recaptured on the summit of the 842 foot hill (distance = feet from summit of 842 foot hill):

7	560	3,200	I-27-67	8	1	8
8	300	3,200	I-8-67	5	1	1
9	140	3,800	II-2-67	4	1	1

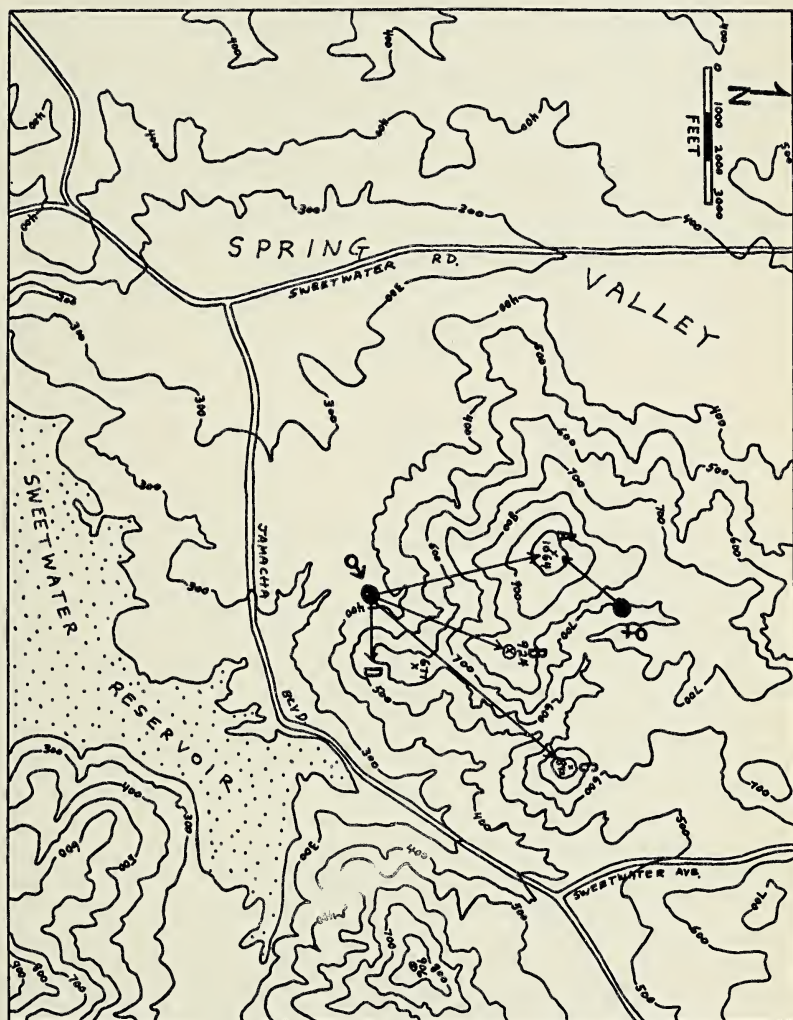


Fig. 11. Release points for reared female (♀) and male (♂) *Papilio zelicaon* and the summits they "homed in" on: A = Dictionary Hill, B = Hill 924, C = Hill 842, D = crest near Hill 677.

Distance travelled (ft.)	Time elapsed (min.)	Speed (ft./min.)
(1) 7,200	155	47
(2) 2,600	34	76
(3) 2,600	31	84
(4) 2,600	19	137

Specimen (1) travelled the distance when no wind was blowing, and specimens (2)-(4) travelled at right angles to a strong westerly wind.

Eighty males from the stock used in the *Papilio zelicaon* female release experiment shortly to be discussed, were released on February 21, 1968, at location 6 (Fig. 12). Twenty-one (26.3%) of these were recaptured on nearby summits:

Location	Vertical feet	Horizontal feet	No. recapt.	Elapsed days to recapture
A	685	4,000	11	2, 2, 2, 2, 2, 3, 3, 3, 3, 4, 4
B	545	3,200	5	4, 7, 7, 11, 18
C	460	5,500	1	9
D	220	1,300	4	7, 7, 8, 8
			21	

Each recaptured male was collected and was not released back into the population. The results show that newly emerged males do not move to the same nearby summit when released from the same location. The individual at location C had to cross a ridge that blocks off location C from the release point. One wonders why the percentage of recapture (26.3%, $N = 80$) should be so similar to recapture for *P. zelicaon* resident males released away from the summit (33.6%, $N = 143$), recaptured resident males (32.4%, $N = 389$), and for recaptured resident males of *Papilio rudkini* (26.7%, $N = 15$).

An experiment was devised to test whether or not virgin females as opposed to recently mated females seek the summit. *Papilio zelicaon* adults reared from eggs were used; the stock came from five females collected *in copula* on the summit of Dictionary Hill, January 11-14, 1968. Their progeny were reared indoors on Sweet Fennel, *Foeniculum vulgare*. Forty-five females were marked and released. Females emerged over a seven-day period prior to the release date of February 21, 1968. After emergence the adults were kept in boxes under refrigeration. One-half (22) of the females were hand-paired to wild-caught and reared males by the technique described by Clarke and Sheppard (1956) and half were left virgin. These two



Fig. 12. Fourteen release points from which *Papilio zelicaon* males collected on Dictionary Hill summit returned to the summit of Dictionary Hill (1064 feet) and Hill 842 (842 feet).

groups were released together late in the afternoon 2,000 feet (385 vertical feet) to the northeast of the summit (Figure 11). During the subsequent four days the summit was intensively collected; the results were as follows:

Date	No. females unmated	No. females mated
Feb. 22	10	1
Feb. 23	3	1
Feb. 24	0	0
Feb. 25	0	1
	13	3

In other words, 59.1 percent of the virgin females and only 13.6 percent of the mated females were recaptured, yet all of these 16 recaptured females proved to be virgin when dissected. Thus the three "mated" females recaptured apparently did not adequately mate when hand-paired, but the high number of unmated recaptures suggests that the mated females not recaptured very likely received a spermatophore when hand-paired.

Percent Virginity

The percent virginity of species from non-hilltop areas varied from 0 to 30 percent, mostly under 10 percent (Table 14). In addition, T. E. Pliske kindly supplied the following unpublished data on percent virginity for species from non-hilltop areas: *Papilio palamedes*, 0.0 percent ($N = 32$); *P. troilus*, 0.6 percent ($N = 358$); *P. glaucus*, 0.0 percent ($N = 171$); *Ascia monuste*, 0.0 percent ($N = 100$); and *Danaus gilippus berenice*, 1.5 percent ($N = 194$). These females were randomly collected at flowers at various places in Florida during the summer of 1961. O. R. Taylor (unpublished) dissected females of many United States and Costa Rican species from non-hilltop situations and found 5 to 20 percent virginity. *Colias* virgin females constituted 10 to 20 percent of the populations ($N > 100$). He was able to obtain virgins of most species where the sample was greater than six.

The high percentages of virgins collected on summits (Tables 15 and 16) are in sharp contrast to samples taken in non-hilltop areas. In 21 hilltopping species where N was less than six, 15 (71.4%) were 67 percent or more virgin. The percentages of virgins in seven species, where N was nine or greater, varied from 0 to 97 percent. (There is some question whether or not *Celastrina argiolus cinerea*, whose percent virginity was zero, is a hilltopping subspecies.) Burns (letter dated June 28, 1967) says that the only virgin female *Papilio glaucus* he has examined ($N > 100$) came from "atop a pronounced escarpment" in Dallas County, Texas.

TABLE 14. Spermatophore counts for species collected in non-hilltop areas

Species	No. spermatophores						Number		0/0
	0	1	2	3	4	5	females	Virgins	
PAPILIONIDAE									
+ <u>Battus philenor</u> (Burns, 1966)	0	17	11	3	1	1	33		0.0
+ <u>Papilio glaucus</u> (Burns, 1966)	0	51	45	14	1	2	113		0.0
+ <u>Papilio multicaudata</u>	0	3	0	1	0	0	4		0.0
+ <u>Papilio zelicaon</u>	3	13	2	0	0	0	18		16.7
+ <u>Parnassius clodius</u> ssp.	"14"	"32"					46		30.4
+ <u>Parnassius phoebus</u> ssp.	"4"	"58"					63		6.5
PIERIDAE									
+ <u>Anthocaris sara</u>	0	20	2	0	0	0	22		0.0
+ <u>Colias eurytheme</u> (Stern and Smith, 1960)	1	76	16	1	0	0	94		1.1
NYMPHALIDAE									
+ <u>Coenonympha tullia</u> ssp.	8	56	4	0	0	0	68		11.8
+ <u>Chlosyne acastus</u>	0	26	1	1	0	0	28		0.0
+ <u>Euphydryas editha</u> (Ehrlich, 1965; Labine, 1966)	1	42	21	0	0	0	64		1.6
+ <u>Poladryas pola</u>	2	9	0	0	0	0	11		22.2
+ <u>Speyeria callippe semivirida</u>	2	51	2	0	0	0	55		3.8
HESPERIIDAE									
+ <u>Polites sabuleti</u> ssp.	2	32	1	0	0	0	35		6.1
+ <u>Pseudocopaeodes eunus</u>	1	24	1	0	0	0	26		4.0
							679		

Reported as new here unless otherwise indicated.

A Spharagus present or absent; no spermatophore count made.

+ One locality only; the other species are from a number of different localities.

TABLE 15. Summary of spermatophore counts for species collected on summits

Species	Number spermatophore					No. in copula with new spermatophore	(C)	
	O(A)						Total no. Females	[(A+B)/C] 0/0 Virgin before reaching summit
	1	2	3	4	5			
<i>Papilio eurymedon</i>	12	2	0	0	0	0	14	85.7
<i>Papilio polyxenes asterius</i>	0	1	0	0	0	0	1	
<i>Papilio rudini</i>	0	2	0	0	0	0	2	
<i>Papilio rutulus</i>	1	0	0	0	0	0	1	
<i>Papilio zelicaon</i>	51	28	3	2	11	0	84	73.8
<i>Anthocaris cethura</i>	14	11	0	0	1	1	25	60.0
<i>Euchloe ausonides coloradensis</i>	0	1	0	1	0	0	2	
<i>Pieris occidentalis calyce</i>	0	0	1	0	1	1	1	
<i>Pieris protodice</i>	2	12	0	0	3	3	14	35.7
<i>Pieris sisymbrii</i>	2	1	0	0	1	1	3	
<i>Chlosyne californica</i>	1	0	0	0	0	0	1	
<i>Euphydryas editha</i>	0	3	0	0	0	0	3	
<i>Euphydryas chalcedona</i>	3	6	0	0	2	0	9	55.6
<i>Speyeria callippe comstocki</i>	1	2	0	0	1	1	3	
<i>Speyeria callippe nevadensis</i>	1	0	0	0	0	0	1	
<i>Vanessa cardui</i>	1	0	0	0	0	0	1	
<i>Vanessa caryae</i>	2	1	0	0	0	0	3	
<i>Callophrys dumetorum</i>	0	2	0	0	2	2	2	
<i>Celastrina argiolus cinerea</i>	0	12	0	0	0	0	12	0.0
<i>Celastrina argiolus echo</i>	4	1	0	0	0	0	5	
<i>Incisalia iroides</i>	3	0	0	0	0	0	3	
<i>Leptotes marina</i>	3	0	0	0	0	0	3	
<i>Erynnis martialis</i>	1	0	0	0	0	0	1	
<i>Erynnis persius</i>	3	2	0	0	0	0	5	
<i>Erynnis propertius</i>	1	0	0	0	0	0	1	
<i>Erynnis tristis</i>	23	15	0	0	14	0	38	97.4
<i>Hesperia miriamae</i>	1	0	0	0	0	0	1	
<i>Hesperia uncas</i>	2	1	0	0	1	1	3	
	132	110				37	242	

* Complete data in Table 16.

TABLE 16. Spermatophore counts of females of
hilltopping species collected on summits *

Papilio eurymedon, 14.

Hill 997 feet, 1.7 mi. SSE El Cajon P. O., San Diego Co., Calif., II-6-67 (O). Cowles Mt., San Diego Co., Calif., VI-6-67 (O). Monument Pk., Laguna Mts., San Diego co., Calif., VI-18-60, leg. R. W. Breedlove (1); V-20-66, leg. S. K. Dvorak (O*); V-7-67 (O). Mt. Kentwood, Laguna Mts., San Diego Co., Calif., V-28-66, leg. R. W. Breedlove (1). Dictionary Hill, Iv-27-57, leg. R. W. Breedlove (O); III-7-65, leg. R. W. Breedlove (O); III-6-66, leg. S. K. Dvorak (O, O); II-5-67 (O); III-12-67 (O); Iv-22-67 (O); II-22-68 (O).

Papilio polyxenes asterius, 1.

Hill by Gates Pass, SW of Tucson, Santa Cruz Co., Ariz., II-22-66, leg. S. K. Dvorak (1).

Papilio rudkini, 2.

"Two Mile Hill," Scissors Crossing, San Diego Co., Calif., II-22-67 (1); IX-14-67 (1).

Papilio rutulus, 1.

Green Mt., Boulder Co., Colo., V-28-66, leg. J. Scott (O).

Papilio zelicaon, 84.

Monument Pk., Laguna Mts., San Diego Co., Calif., V-28-66, leg. R. W. Breedlove (1). Mt. Kentwood, Laguna Mts., San Diego Co., Calif., V-28-66, leg. R. W. Breedlove (O). Green Mt., Boulder Co., Colo., V-28-66, leg. J. Scott (1). Escalante Overlook, 7500', Dinosaur National Monument, Moffat Co., Colo., VI-9-67, leg S. Ellis (O). Dictionary Hill, II-22-66, leg. R. W. Breedlove (O); X-25-66 (1, 1); XII-17-66 (O, O); XII-18-66 (O, O, O, 1); XII-19-66 (O, O, 1); XII-24-66 (O, O); XII-25-66 (O, O, O); XII-26-66 (2); XII-28-66 (O, O, 1); XII-31-66 (O, 1*); I-1-67 (O*); I-7-67 (O); I-9-67 (O); I-14-67 (O, O, O); I-15-67 (O, O, 3); I-27-67 (1); I-28-67 (O); II-4-67 (O, O, O, 1); II-12-67 (1); II-22-67, leg. R. W. Breedlove, (O*); II-26-67 (O, O); III-5-67 (O); III-16-67 (1); III-19-67 (1, O); IV-23-67 (O*); IV-30-67 (O); V-1-67 (O); V-4-67 (O*); IX-13-67 (1, 2, 2); IX-28-67 (O, 1*); XII-17-67 (1*); XII-22-67 (O, O* 1*); XII-23-67 (O); XII-27-67 (1); I-1-68 (1*); I-11-68 (1*); I-13-68 (1*, 1*, 1*); I-14-68 (1*); I-21-68 (O*); I-29-68 (O); II-2-68, leg. G. Forbes (O); II-19-68 (1); II-22-68 (O); II-23-68 (O); II-24-68 (O, O, 1, 3); III-10-68 (1*). Hill 906 feet, 1.8 mi. SE Dictionary Hill, III-3-68 (O, 1).

Anthocaris cethura, 25.

Dictionary Hill, II-12-67 (1); II-20-67 (O); II-28-67 (1, 1); III-5-67 (O); III-12-67 (1); III-16-67 (O*) III-25-67 (1); IV-8-67, leg. R. W. Breedlove (O, O); Iv-22-67 (O);

TABLE 16 (continued)

IV-23-67 (O); IV-27-67 (O); V-4-67 (O); V-14-67 (O);
 II-22-68 (1); II-23-68 (O); II-25-68 (1); II-26-68 (1); leg. S. K. Dvorak,
 III-21-68 (1). Tectate Mt., San Diego Co., Calif., IV-9-67 (O);
 V-20-67 leg. R. W. Breedlove (1). Hill 997 feet, 1.7 mi. SSE
 El Cajon P. O., San Diego Co., Calif., IV-27-58 (1); III-15-59 (O);
 III-21-59 (O).

Euchloe ausonides coloradensis, 2.

East end of S. Table Mt., Jefferson Co., Colo., V-20
 to 22-66, leg. J. Scott (1, 3).

Pieris occidentalis calyce, 1.

Ridge above Cottonwood Pass, Chaffee Co., Colo.,
 VII-26-67 (2*),

Pieris protodice, 14.

Dictionary Hill, XII-17-66 (1); XII-19-66 (1, 1);
 XII-28-66 (1); XII-29-66 (O); I-15-67 (1); II-2-67 (1);
 II-20-67 (1*); III-30-67 (1); V-14-67 (1); VI-9-67 (1);
 I-13-68 (O). Hill 842 feet, E. of Dictionary Hill,
 I-9-67, leg. F. T. Thorne, (1). Tecate Mt., San Diego Co.,
 Calif., V-20-67, leg. F. T. Thorne, (1).

Pieris sisymbrii, 3.

Mt. Kentwood, Laguna Mts., San Diego Co., Calif.,
 IV-30-66, leg. S. K. Dvorak (1*); V-7-67 (O). Tecate
 Mt., San Diego Co., Calif., III-28-64, leg. S. K.
 Dvorak (O).

Chlosyne californica, 1.

"Two Mile Hill," Scissors Crossing, San Diego Co.,
 Calif., II-18-67 (O).

Euphydryas editha, 3.

Dictionary Hill, III-30-67 (1); II-23-68 (1, 1).

Euphydryas chalcedona, 9.

Dictionary Hill, II-26-67 (O); III-19-67 (1); IV-17-67
 (1, 1*); IV-27-67 (O); V-2-67 (1); V-6-67 (1*); V-14-
 67 (1). Tecate Mt., San Diego Co., Calif., IV-9-67 (O).

Speyeria callippe comstocki, 3.

Dictionary Hill, IV-16-67 (O); V-14-67 (1). Cowles
 Mt., San Diego Co., Calif., VI-6-67 (1*).

Speyeria callippe nevadensis, 1.

Buckskin Mt., Santa Rosa Range, Humboldt Co., Nev.,
 VIII-11-67 (O).

Vanessa cardui, 1.

Dictionary Hill, I-6-67 (O).

Vanessa caryae, 3.

Dictionary Hill, III-5-67 (O); V-1-67 (1); V-14-67 (O).

Callophrys dumetorum, 2.

Dictionary Hill, III-16-67 (1*); III-25-67 (1*).

TABLE 16 (continued)

Celastrina argiolus cinerea, 12.

Green Mt., Boulder Co., Colo., V-30-65 (1, 1, 1, 1, 1);
V-25-66 (1, 1); V-28-66 (1, 1, 1, 1, 1); all leg. J. Scott.

Celastrina argiolus echo, 5.

Dictionary Hill, IV-22-67 (O); V-6-67 (O*). Hill 842
feet, E. of Dictionary Hill, II-4-67, leg. R. W. Breed-
love (O). Tecate Mt., San Diego Co., Calif., IV-29-61
(O); IV-23-66, leg S. K. Dvorak (1).

Incisalia iroides, 3

Dictionary Hill, II-13-67 (O); IV-23-67 (O); II-24-68 (O).

Leptotes marina, 3.

Dictionary Hill, III-30-67 (O*); IV-16-67 (O);
IV-27-67 (O).

Erynnis martialis, 1.

Green Mt., Boulder Co., Colo., V-28-66, leg. J. Scott
(O).

Erynnis persius, 5.

Hilltop, Coal Creek Canyon, Jefferson Co., Colo., VI-6-
65, leg. J. Scott (O, O, 1). Genesee Mt., Jefferson
Co., Colo., VI-10-66, leg. J. Scott (1). Wildcat Mt.,
Douglas Co., Colo., V-21-67, leg. J. Scott (O).

Erynnis propertius, 1.

Dexter Pk., Cuyamaca Mts., San Diego Co., Calif.,
V-7-67, leg. R. W. Breedlove (O).

Erynnis tristis, 38.

Hilltop 997 feet, 1.7 mi. SSE El Cajon P.O., San Diego
Co., Calif., II-6-67 (O, O*, 1). Dictionary Hill,
I-15-67 (O); I-26-67 (O); I-27-67 (1); II-2-67 (O*, O*, O*,
1); II-4-67 (O, O*, 1); II-5-67 (O); II-11-67
(1*, 1*); II-16-67 (O); II-22-67 (1*, 1); II-26-67
(O, O*, O*, 1*, 1); II-27-67 (O, 1*, 1); II-28-67
(1*); III-16-67 (O*, O*, 1*); V-14-67 (O); II-22-68
(O*); II-23-68 (O*, O*); II-24-68 (O*); II-25-68 (O*, 1*).

Hesperia miriamae, 1.

Unicorn Pk., Yosemite National Park, Calif., VIII-12-58
(O*).

Herperia uncas, 3.

Hilltop 4 mi. S. of Gunnison, Gunnison Co., Colo.,
VII-2-67 (O); VII-20-67 (O, 1*).

* Each number in parentheses is the number of
spermatophore (s) for an individual female. These were
collected by me unless otherwise indicated. Those with
an asterisk were taken in copula.

This high percentage of virgins is what one would predict if summit congregations serve a meeting purpose for the sexes, since non-virgins in species that mate but once would not seek summits to mate. Single mating exists in certain butterflies in eastern North America (Burns, 1966). However, one would also expect that non-virgin females might also seek summits in species that mate more than once, as in *Papilio* (Burns, 1966), and *Euphydryas* (Labine, 1966). It is significant that the three lowest percentages (excluding *Celastrina argiolus cinerea*) of virgin females on summits (36, 56, and 60) were for species that were seen to oviposit on and near the summit as well as in other areas, so that ovipositing and mate-seeking females were probably both present on the summit in these species.

Non-hilltopping species were rarely encountered on summits (Tables 17 and 18). The only such species taken in numbers, *Anthocaris sara* ($N = 18$) and *Pieris rapae* ($N = 10$), showed no virginity, as did four of the six other species.

Female Rarity

It is evident from marking experiments that males of *Papilio zelicaon* will remain for long periods of time on the summit on a given day and will return to hilltop for a number of days. Presumably, virgin females will arrive at the summit for one day only, and then only long enough to mate. Females of *in copula* pairs watched until they uncoupled always flew downhill a short time after termination of copulation. On a given day one would expect a lower number of females than males to be present on the summit, assuming that both sexes are emerging from pupae in about equal numbers over an extended period of time. Butterflies apparently do emerge in about one-to-one sex ratio (Table 19). During periods of low male density, the females would be more easily noticed than during periods of high male density because *in copula* pairs would be more rapidly formed when many males are territorial. *In copula* pairs were mostly found by observing initial courtship; few were discovered already *in copula*. Most pairs mate downslope after flying from the summit and are difficult to locate because of the large area to search for them.

A comparison of the number of females of *P. zelicaon* present with the number of males marked and recaptured during periods of low and high density was made over two 30-day periods. During December 17, 1966 to January 15, 1967, there was a period of low male density; 57 were marked on 18 different days. During that time 29 females were captured and three were

TABLE 17. Summary of spermatophore counts for non-hilltopping species

Species	Number spermatophores				(B) No. in copula with new Spermatophore	(C) Total no. females	[(A+B)/C]
	O(A)	1	2	3			
<u>Anthocaris sara</u>	0	16	2	0	0	18	0.0
<u>Zerene cesonia</u>	0	1	0	0	0	1	
<u>Eurema nicippe</u>	0	2	0	0	0	2	
<u>Pieris rapae</u>	0	9	1	0	0	10	0.0
<u>Coenonympha tullia</u>	0	1	0	0	0	1	
<u>Chlosyne gabbi</u>	1	0	0	0	0	1	
<u>Everes comyntas</u>	0	2	0	0	0	2	
<u>Erynnis funeralis</u>	1	3	0	0	0	4	
	2	<u>37</u>			<u>0</u>	<u>39</u>	

TABLE 18. Spermatophore counts of females of non-hilltopping species collected on summits

Anthocaris sara, 18.

Dictionary Hill, San Diego Co., Calif., IV-10-66, leg. R. W. Breedlove (1); II-12-67 (1, 1); II-27-67 (2, 1); II-28-67 (2); IV-30-67, leg. R. W. Breedlove (1); V-14-67 (1, 1, 1, 1); V-15-67 (1, 1); II-25-68 (1, 1). Hill 842 feet, E. of Dictionary Hill, II-3-67, leg. S. K. Dvorak (1). Tecate Mt., San Diego Co., Calif., IV-28-66, leg. R. W. Breedlove (1). "Two Mile Hill," Scissors Crossing, San Diego Co., Calif., II-18-67 (1).

Zerene cesonia, 1.

Hill 906 feet, 1.8 mi. SE Dictionary Hill, IV-11-68 (1).

Eurema nicippe, 2.

Dictionary Hill, I-15-67; II-25-68 (1).

Dictionary Hill, I-15-67 (1); II-25-68 (1).

Pieris rapae, 10.

Dictionary Hill, I-19-66 (1); II-19-68 (1); II-22-68 (1); II-23-68 (1, 1, 1); II-24-68 (1); II-25-68 (1, 1, 2).

Coenonympha tullia, 1.

Dictionary Hill, II-25-68 (1).

Chlosyne gabbi, 1.

Dictionary Hill, III-30-67 (O).

Everes comyntas, 2.

Dictionary Hill, II-24-68 (1); II-25-68 (1).

Erymnis funeralis, 4

Dictionary Hill, VI-9-67 (O); II-24-68 (1); II-25-68 (1, 1).

TABLE 19. Approximate 1:1 sex ratios for butterfly species reared in numbers

Species	Number males	Number females	Source	Reference
PAPILIONIDAE				
<u>Graphium marcellus</u>	--	--	eggs	Heitzman, in litt. +
<u>Papilio eurymedon</u>	--	--	eggs	Thorne, pers. comm.
<u>P. glaucus</u>	24	27	eggs	Kendall, i. l.
<u>P. indra fordi</u>	5	5	--	Henne, P. c.
<u>P. palamedes</u>	30	33	eggs	Kendall, 1964
<u>P. polyxenes asterius</u>	24	24	eggs	Kendall, i. l.
<u>P. rudkini</u>	65	73	eggs	Hedges, p. c.
<u>P. zelicaon</u>	--	--	eggs	Thorne, p. c.
PIERIDAE				
<u>Nathalis iole</u>	8	8	eggs	Henne, p. c.
<u>Pieris protodice</u>	13	11	--	Kendall, i. l.
NYMPHALIDAE				
<u>Asterocampa celtis</u>	78	83	eggs	Heitzman, i. l.
<u>A. clyton</u>	65	74	eggs	Heitzman, i. l.
<u>Chlosyne ismeria</u>	124	133	eggs	Kendall, 1964
<u>Danaus plexippus</u>	--	--	eggs	Urquhart, 1960
<u>Euphydryas chalcedona</u>	--	--	eggs	Thorne, p. c.
<u>E. editha bayensis</u>	--	--	eggs	Ehrlich, 1965
<u>E. phaeton</u>	16	18	eggs	Heitzman, i. l.
<u>Phyciodes tharos</u>	28	24	eggs	Kendall, 1964
<u>Polygonia interrogationis</u>	159	143	eggs	Kendall, i. l.

TABLE 19 (continued)

Species	Number males	Number females	Source	Reference
LYCAENIDAE				
<u>Atides halesus</u>	36	36	eggs	Thorne, p. c.
<u>Calephelis perditalis</u>	34	43	eggs	Kendall, i. l.
<u>C. rawsoni</u>	147	138	eggs	Kendall, i. l.
<u>Callophrys xami</u>	59	69	eggs	Kendall, i. l.
<u>Incisalia henrici solatus</u>	27	25	eggs	Kendall, 1965
<u>Mitoura johnsoni</u>	12	12	eggs	McCorkle, i. l.
<u>Philotes mohave</u>	--	--	eggs	Henne, p. c.
<u>P. rita elvirae</u>	--	--	eggs	Henne, p. c.
<u>P. enoptes</u>	--	--	eggs	Henne, p. c.
HESPERIIDAE				
<u>Amblyscirtes linda</u>	31	33	eggs	Heitzman, i. l.
<u>A. vialis</u>	14	12	eggs	Heitzman, i. l.
<u>Copaeodes aurantiaca</u>	16	13	eggs	Kendall, 1965
<u>Erynnis horatius</u>	121	111	eggs and larvae	Kendall, 1965
<u>Gesta gesta invisus</u>	64	71	larvae	Kendall, 1965
<u>Megathymus yuccae</u>	532	473	and pupae from 120	Roever, i. l.
<u>Thorybes pylades</u>	20	21	populat. eggs	Kendall, 1965

"--" = numbers not available but ratio was 1:1

+ = in a letter.

sighted for a total of 32 females, or 56.1 percent of the total male population. During February 11, 1967 to March 12, 1967, there was a period of high male density; 123 were marked on 15 different days. During that time only five females were captured, or only 4.1 per cent of the total male population. Thus, during times of low density populations there may be more than half as many females as males present. Due to the difficulty of finding females *in copula*, as many females as males may actually have been present.

The population of *Papilio eurymedon* on Dictionary Hill is low in density compared to certain other summits in San Diego County, where males are frequently plentiful. Dictionary Hill is probably on the periphery of its range. During January to May 1967 only 12 different males were marked, collected, or seen on the summit, and three females were collected and one seen for a total of four females, or 33.3 percent of the total male population.

Female Behavior and Mating

Papilio zelicaon. These observations are based primarily on 77 females (58 virgin, 19 non-virgin) collected on Dictionary Hill summit. They were collected while in flight or alighted; 17 *in copula* pairs were collected and other courting and mated pairs were observed. Wing condition, as expected, showed a high correlation with mated condition; virgins almost exclusively had a fresh wing condition while most non-virgins had a fair to worn wing condition. Only one of the non-virgins had a freshly deposited spermatophore; the remainder had spermatophores that were collapsed. Frequently virgin females' genital regions were expanded when captured.

All females collected appeared on the summit during the time when males were resident and well after the males had established territories for the day. Females on the summit usually flew quite slowly; virgin females with fresh wing condition characteristically had a slow, fluttering flight, generally in areas occupied by males. When all or nearly all of the resident males were collected, females flew back and forth over the summit, occasionally alighting on the ground or vegetation; three females stayed on the summit for six, seven, and eleven minutes respectively in these lingering flights. Females that were frightened off the summit by a swing of the net flew downslope but generally returned within a few minutes.

(Edwards [1884] reported the flight behavior of a female

Papilio brevicauda on a mountain top at Topsail, Newfoundland: "It made long flights, rarely alighting, but apparently reconnoitering the whole mountain." The female was probably a virgin since she laid infertile eggs when confined.)

Virgin females, including two taken *in copula*, often had pollen adhering to their bodies and were twice noted to visit flowers before flying to the summit.

Courtship stages were seen in twelve pairs. The females flies into an area where males are perched or patrolling; the male immediately investigates her and responds by fluttering close behind her in a bobbing flight. At times this flight is done immediately in front of the female. Presumably during this flight the male is emitting a pheromone. Males as old as four weeks have a sweet pungent odor, while freshly emerged males do not. Copulation itself may take place downslope or on the summit. *In copula* pairs were found either slightly downslope (as far as 125 yards from the summit) or on the summit. The female alights at the edge of the summit or usually slightly downslope. The time the pair first meets to when their genitalia are in contact usually takes about one to three minutes. The male alights behind and parallel to the female or underneath the females and curves his abdomen until their genitalia are in contact. He then establishes a position to that each is facing in opposite directions and oriented with their backs to the sun. In most cases the female's wings are shut or partially open and the male's wings are opened flat. Pumping motions of the male's abdomen last for a few minutes. In one pair the female used her back legs to stroke the male's abdomen and genitalia intermittently. Pairs found *in copula* were resting on vegetation one to four feet off the ground (Fig. 13). The female carries the quiescent male when the pair is disturbed. The male initiates the uncoupling of the *in copula* pair.

One attempted courtship by more than one male was rejected by a virgin female. From one to four males chased the female. The female flew rapidly rather than slowly fluttering when pursued. Once a female broke into a fluttering, falling flight when closely investigated by a male *Vanessa atalanta*.

Anthocaris cethura. Fourteen females were collected on or near the summit of Dictionary Hill; of these, nine were virgins and five were non-virgins. Three females were taken *in copula*. Virgin females were mostly taken while in flight or when they had alighted in areas where males patrolled. One virgin female was collected feeding on a flower on the summit.

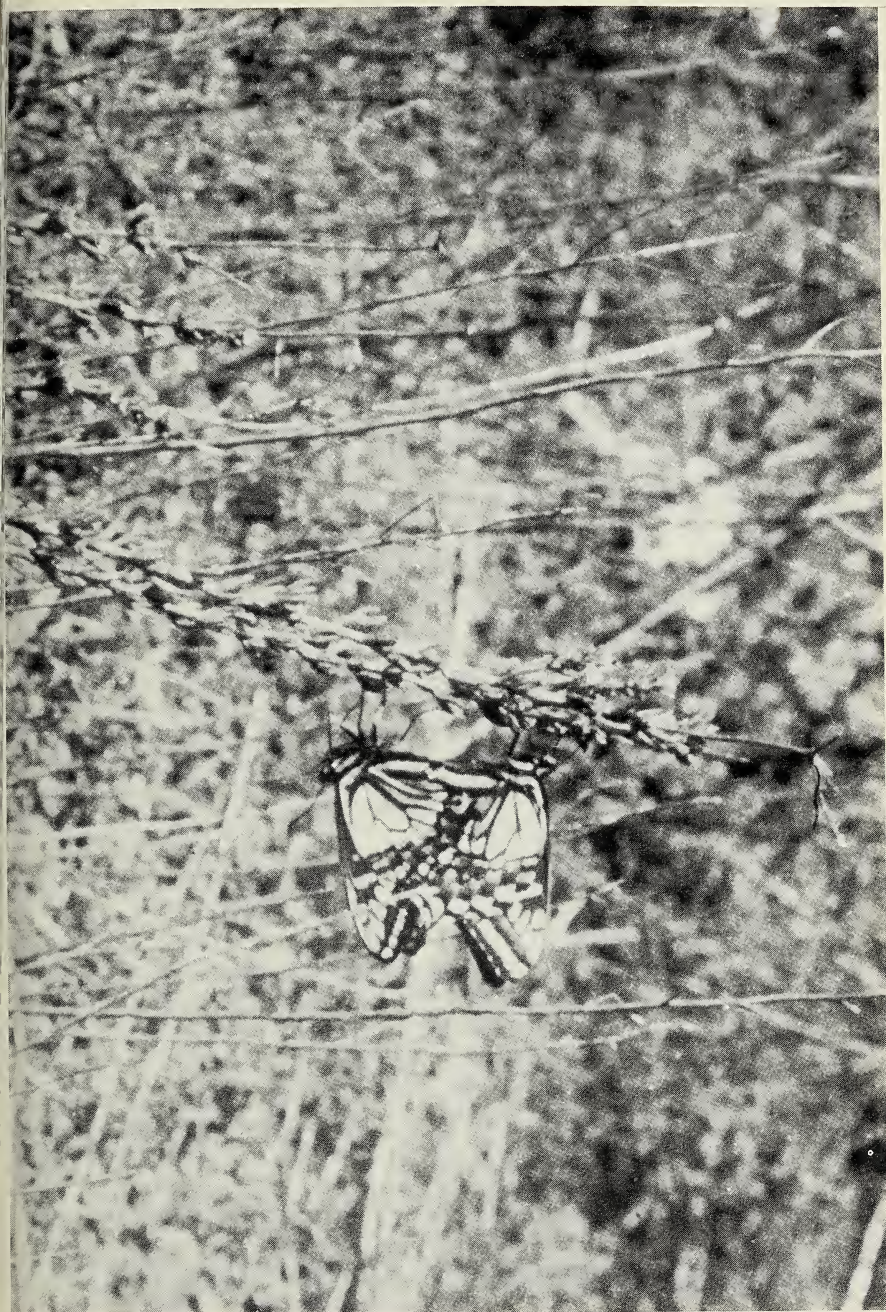


Fig. 13. In copula pair of *Papilio zelicaon*.

A virgin female was observed on the summit from 1009-1018 hours on April 27, 1967. During this time the female alighted four times (for periods of two minutes, three-and-one-half minutes, one minute, and one minute respectively) on vegetation in areas along a 100-foot strip where males in the past had patrolled. When perched, the female flew up to meet two passing male *Pieris protodice* and once flew up after a male *Speyeria callippe comstocki*. In both cases the *protodice* briefly courted the female but separated after five to ten seconds. At 1018 the female was collected.

A pair *in copula* was taken resting three feet up on vegetation on the summit at 1209, March 16, 1967. The female was positioned downward and the male upward. The male carried the quiescent female when the pair was disturbed. Another pair was taken *in copula* on March 21, 1968, at 1050. The female contained a collapsed spermatophore indicating that she was mating for the second time.

Mating was seen with one female on February 28, 1967. At 1023 and 1102 hours fresh virgin females appeared at a rock outcropping area which males frequent on the summit. One of these was immediately collected and the other was observed. The observed female fluttered in an area with many nectar sources for about one minute and alighted on these plants without feeding. The female then alighted on some grass, perched facing upwards, and remained there, with wings shut, one foot off the ground. A marked male with fair wing condition, which had been recaptured three times on the same day, flew by the area and immediately dropped down to the female, alighting parallel to her, and initiated copulation. The female then positioned herself so that the male faced up and she faced down. The pair remained in this position with wings shut for six minutes, during which time a spermatophore was passed as shown by later dissection. Four different males, two of which were collected, flew by the area. In each case, the male suddenly dropped down to the mated pair, attempted copulation for about ten seconds, then flew off. The female may have emitted a pheromone that attracted males who were in close proximity, or the male's response may have been strictly visual. After six minutes the pair was collected.

On March 25, 1967, two non-virgin females were collected very near the summit during oviposition behavior. One oviposited on tansy mustard, *Descurainia pinnata*, a known foodplant that grows up to the summit of Dictionary Hill. The other female

hovered over black mustard, *Brassica nigra* plants, alighted on one small mustard plant, and curled her abdomen toward the plant; however, no egg was found.

Pieris protodice. Observations are based on eleven females collected on Dictionary Hill summit: two virgins and nine non-virgins. One of the virgins was captured feeding on a flower, and the other was taken *in copula*. Two of the non-virgins were taken in oviposition behavior directed toward young *Brassica nigra* plants.

Abbott (1959:288) described in detail the courtship and mating of *P. protodice* in Texas. One non-virgin female on Dictionary Hill summit displayed acceptance behavior toward a hovering male (0854, May 14, 1968): i.e., wings spread and abdomen elevated while resting on vegetation. A female with a freshly deposited spermatophore exhibited rejection behavior toward a courting male (1258, February 3, 1967, on Hill 842, east of Dictionary Hill). The female, pursued by a male, alighted on the ground. The male alighted alongside of the female and tried unsuccessfully to make genitalia contact. He then walked around in front of the female, faced her, and flew off. An *in copula* pair taken at 1058, February 20, 1967, on Dictionary Hill summit, was located because two males alighted by the pair. In two *in copula* pairs the male carried the quiescent female when the pair was disturbed.

Vanessa species. Despite numerous observations of male encounters in hilltopping *Vanessa* species, only two courtships of females were observed. This inability to observe mating pairs was probably due to the formation of *in copula* pairs in the late afternoon when few observations were made. The two courtships occurred at 1513 and 1533 hours on January 6, 1967, only two hours before sunset. *Vanessa* mating times have been reported as 4:15 p.m. for *V. atalanta*, 6 p.m. for *V. cardui* (both Pronin, 1964), and 8:30 p.m., D.S.T. for *V. cardui* (Temple, 1953). The two pairs observed in courtship were *V. cardui* and *V. caryae*. In both cases the courting pair alighted on the ground with the male behind the female and were then collected.

Strymon melinus and *Incisalia iroides*. No matings of these two species were observed. *I. iroides* males were only occasionally seen, but *S. melinus* males were frequently encountered in the afternoons. Again, probably the reason no matings were observed was that pairs may have formed in the late afternoons when few observations were made. Reinhard (1929) states that

S. melinus mated in Texas cotton-fields "late in the evening or shortly before sunset." Powell (1964a) noted that four pairs of *I. iroides* mated on a lemon tree only after 4:00 p.m., P.S.T.

Callophrys dumetorum. Two *in copula* pairs were collected on the summit of Dictionary Hill. At 1018, March 25, 1967, an *in copula* pair, both sexes with fresh wing condition, was found on an unopened composite flowerhead two feet above the ground. Both individuals were horizontal with wings folded, broadside to the sun. Their resting site was at the edge of a clearing where a male was exhibiting territorial behavior.

Courtship and mating were observed with a pair at 1010, March 16, 1967. A virgin female with fresh wing condition flew from the north into a male's territory on the summit. The male, which was perched and had a worn wing condition, flew up to investigate the female and hovered behind her. The female then alighted almost immediately two-and-one-half feet up on vegetation and quivered her partly opened wings. The male alighted parallel and slightly behind the female, curved his abdomen around, engaged genitalia, and positioned himself so that he faced downward and the female upward. All these actions happened rapidly. The pair faced the sun and had their wings closed. After nine minutes the pair was collected; a spermatophore had been passed during that time.

Erynnis tristis. Females were difficult to distinguish from males in flight. They were recognized as females only when *in copula* and during courtship. Essentially all of the 35 females collected on the summit were virgin and had fresh wing condition. All but one of the 14 females with freshly deposited spermatophores were taken *in copula* on the summit. All females appeared when males were actively hilltopping.

Courtship stages were seen partially or completely in six different pairs. The virgin female flies into a male's territory on the summit. The male flies off his perch to investigate the female and flutters behind and below her, occasionally rising up and making apparent contact. The female responds by alighting on vegetation one to four feet above ground (a rock in one instance served as the substrate). The male immediately alights parallel and slightly behind the female and curves his abdomen to make genitalia contact. Upon engagement the male positions himself so that he is facing down and the female faces up. Females which were closely examined at this stage had numerous scales along the shaft and nudum of their antennae. These were probably androconial scales from the male's coastal fold deposited

during the brief "contacts" before alighting. Burns (1964:88) predicted that these scales "probably serve a communicative function during courtship." The female next grasps the substrate rapidly with her legs and begins to brush off the scales along the shafts of her antennae with her front legs. Next, either the left or right leg of the female twitches rapidly, sometimes out and back and sometimes in apparent contact with the pair's genitalia region. The tip of this leg has a tuft of hairs not present on the other hind leg. I did not notice where these hairs were taken from. This leg twitching is intermittent and lasts about three minutes. Finally, the female cleans all the scales off her antennae with her front legs, at the same time rubbing her eyes and coiling and uncoiling her proboscis. The male is quiescent during all of these motions except for rhythmic contractions of his abdomen. Soon the pair ceases all motions and rests in a position about 30 degrees from the horizontal (Fig. 14). These motionless pairs could be approached quite closely, although several times such a pair took flight after prolonged close observation. Such flights extended 10 to 50 feet away, the female always carrying the quiescent male.

All of the *in copula* pairs noted (18) that were not seen in courtship were found resting in or near a known male territorial area. Frequently, passing males would investigate such a pair and attempt copulation but would leave very shortly. All pairs were perpendicular to the sun's rays. On sunny days a quiescent pair would have their wings closed, but on overcast days or during the passage of a cloud across the sun their wings were expanded.

Excessive numbers of males apparently terminated one courtship. At 1355, February 12, 1967, a female was seen pursued by two males. The female alighted several times on branches but each time flew off. A third male joined the chase when the group passed through his territory. At this point the female flew rapidly off with the three males in pursuit. Momentarily the group was lost from sight, but shortly the three males returned chasing each other. The whole encounter took about three minutes.

A rejection flight by a freshly mated female was seen at 1400, January 27, 1967. A male fluttered behind the female. The female rose high into the air, and the male rose behind her, touched her, and returned to ground level. Immediately the female returned to ground level, where the same process was repeated. The female then alighted on a bush and was collected; she contained a freshly deposited spermatophore.



Fig. 14. *In copula* pair of *Erynnis tristis*.

Behavior of Sexes after Uncoupling

The behavior of eight *Papilio zelicaon* pairs after uncoupling on the summit was observed. If conditions were warm or mild, the females flew rapidly and continuously downhill until lost from sight; one such female was followed for one-third mile. On cool days the females unusually sunned for awhile before flying downhill; their flight was much slower with frequent alightings on vegetation to sun themselves. In all cases the females departed from the summit and did not fly around the summit like the virgin females. Departing females flew into and at random angles to the wind. Males resumed hilltopping behavior shortly after uncoupling. In one instance the male that had uncoupled from a pair 375 feet from the summit was found 20 minutes later *in copula* with another female at the summit.

Two *Erynnis tristis* pairs were observed after uncoupling on the summit on a cool, overcast day (February 19, 1968). In both cases the female sunned on the ground for several minutes before rapidly flying off the summit. With one of these pairs, arrival, copulation, and departure of the female was seen during a 61-minute period; the male resumed territorial behavior in his original territory two minutes after uncoupling.

Larval Foodplant Proximity

Tables 20 and 21 give the known larval foodplants for hilltopping and non-hilltopping species and whether they are located near or far away from the summit of Dictionary Hill. There was no difference in the percentage of hilltopping and non-hilltopping species whose foodplants were near or far, as measured arbitrarily from the 900-foot contour line (distance from the summit to the line is 400 to 1,400 feet and 164 vertical feet):

	Larval foodplant present above 900-foot contour		
	Present	Absent	% Absent
Hilltoppers	14	7	33.3
Non-hilltoppers	17	8	32.0

Certain hilltopping species had to fly a moderate distance to hilltop. *Papilio eurymedon*'s nearest foodplant source is a colony of about twenty *Rhamnus crocea* bushes 1,600 to 2,100 feet to the east (300 vertical feet). *Erynnis tristis* feeds on *Quercus agrifolia* (Burns, 1964). The nearest *Q. agrifolia* tree is 2.6 miles away, the first area of concentration is 3.1 miles away, and the main center of concentration is 3.8 miles away to the east. *Quercus dumosa* also grows in the area and may be a possible foodplant. The first bushes (five) of *Q. dumosa* are 1,900 feet away and

TABLE 20. Foodplants for hilltopping species on Dictionary Hill

Species	Larval foodplant present on slopes above 900' contour	Known possible foodplants available in the area
1. <u>Battus philenor</u>	absent	<u>Aristolochia</u> sp.
2. <u>Papilio eurymedon</u>	absent	<u>Ceanothus</u> sp., <u>Rhamnus californica</u> , <u>R. crocea</u> , <u>Prunus</u> sp.
3. <u>Papilio zelicaon</u>	absent	<u>Foeniculum vulgare</u> , <u>Daucus</u> sp.
4. <u>Anthocaris cethura</u>	present	<u>Descurainia</u> sp., maybe <u>Brassica nigra</u>
5. <u>Pieris protodice</u>	present	<u>Brassica nigra</u> , <u>Raphanus</u> sp.
6. <u>Chlosyne leanira</u> <u>wrightii</u>	present	<u>Castilleja</u> sp. λ
7. <u>Euphydryas editha</u>	present	<u>Plantago Hookeriana</u> var. <u>californica</u>
8. <u>Euphydryas chalcedona</u>	present	<u>Scrophularia californica</u>
9. <u>Speyeria callippe</u> <u>comstocki</u>	present	<u>Viola pedunculata</u>
10. <u>Vanessa atalanta</u>	absent	<u>Urtica urens</u> , thistles
11. <u>Vanessa cardui</u>	present	Boraginacea, Compositae, Malvaceae (<u>Malva parviflora</u> preferred)
12. <u>Vanessa caryae</u>	present	<u>Malva parviflora</u> preferred, other Malvaceae
13. <u>Vanessa virginiensis</u>	present	<u>Gnaphalium</u> sp., other Compositae
14. <u>Atlides halesus</u>	absent	<u>Phoradendron flavescens</u>
15. <u>Callophrys dumetorum</u>	present	<u>Eriogonum fasciculatum</u> , <u>Lotus scoparius</u>
16. <u>Celastrina argiolus</u> <u>echo</u>	present	<u>Ceanothus</u> sp., <u>Lotus</u> sp.
17. <u>Incisalia iroides</u>	present	<u>Cuscuta</u> sp., <u>Ceanothus</u> sp., <u>Sedum</u> sp.
18. <u>Leptotes marina</u>	present	<u>Astragalus</u> sp., <u>Plumbago</u> sp.
19. <u>Satyrium saepium</u>	absent	<u>Cercocarpus betuloides</u> , <u>Ceanothus</u> sp.
20. <u>Strymon melinus</u>	present	many
21. <u>Erynnis tristis</u>	absent	<u>Quercus agrifolia</u>

Foodplants compiled from Comstock (1927), Klots (1951), Emmel and Emmel (1963b), Garth and Tilden (1963), Burns (1964), and Thorne (pers. comm.). Higgins (1949) was used as an aid to finding certain plant locations.

λ Butterfly no longer present.

TABLE 21. Foodplants for non-hilltopping species
on Dictionary Hill

1. <u>Anthocaris sara</u>	present	<u>Brassica nigra</u>
2. <u>Colias eurytheme</u>	present	<u>Medicago sativa</u> , less frequently other legumes
3. <u>Colias harfordii</u>	present	<u>Astragalus</u> sp.
4. <u>Zerene cesonia</u>	present	<u>Amorpha</u> sp., <u>Trifolium</u> sp.
5. <u>Eurema nicippe</u>	absent	<u>Cassia</u> sp.
6. <u>Pieris rapae</u>	present	<u>Brassica nigra</u> , cultivated Cruciferae
7. <u>Phoebis sennae</u>	absent	<u>Cassia</u> sp.
8. <u>Danaus gilippus</u> <u>berenice</u>	absent	<u>Asclepias</u> sp.
9. <u>Danaus plexippus</u>	absent	<u>Asclepias</u> sp.
10. <u>Coenonympha tullia</u> <u>californica</u>	present	Gramineae
11. <u>Agraulis vanillae</u>	absent	<u>Passiflora</u> sp.
12. <u>Chlosyne gabbi</u>	present	<u>Corethrogyne</u> sp., <u>Hazardia</u> sp.
13. <u>Junonia coenia</u>	present	<u>Plantago</u> sp., <u>Gnaphalium</u> sp.
14. <u>Nymphalis antiopa</u>	absent	<u>Ulmus</u> sp., <u>Salix</u> sp., <u>Populus</u> sp.
15. <u>Apodemia mormo</u> <u>virgulti</u>	present	<u>Eriogonum fasciculatum</u>
16. <u>Brephidium exilis</u>	present	<u>Atriplex</u> sp., <u>Chenopodium</u> sp.
17. <u>Everes comyntas</u>	present	<u>Astragalus</u> sp., <u>Trifolium</u> sp.
18. <u>Glaucopsyche lygdamus</u>	present	<u>Lotus scoparius</u> , <u>Astragalus</u> sp.
19. <u>Lycaena helloides</u>	absent	<u>Rumex</u> sp., <u>Polygonum</u> sp.
20. <u>Philotes battoides</u> <u>bernardino</u>	present	<u>Eriogonum fasciculatum</u>
21. <u>Erynnis funeralis</u>	present	<u>Lotus scoparius</u> , <u>Medicago sativa</u> , <u>Nemophila membranacea</u>
22. <u>Heliopetes ericetorum</u>	present	<u>Malvastrum</u> sp., <u>Amaranthus</u> sp.
23. <u>Hylephila phyleus</u>	absent	<u>Cynodon Dactylon</u>
24. <u>Ochlodes sylvanoides</u>	present	Gramineae
25. <u>Pyrgus communis</u>	present	Malvaceae

the first area of concentration is 4,600 feet away to the east. *Erynnis tristis* belongs to a superspecies of *Quercus* feeders; no other foodplants are known for the group (Burns, 1964). Freshly emerged *Papilio zelicaon* males hilltopped as far as 5,500 feet away from the release point.

Three hilltopping species were seen to oviposit on the summit: *Anthocaris cethura*, *Pieris protodice*, and *Euphydryas chalcedona*. Since they do oviposit as well as mate on the summit, the percentage of virgin females for these species would be less than expected if only mating took place. These three species did have the lowest percentages of virginity of the hilltopping species present (see Table 15) yet were still above the highest percent virginity for non-hilltop areas.

Species Approach to the Summit

Instances of actual flight to the summit by hilltopping species were watched for although rarely observed. Particular attention was given to local wind conditions when species did approach the summit, in view of the emphasis placed by various authors on updrafts and winds as causative agents in hilltopping.

Male *Papilio zelicaon* were twice noted at distances greater than 100 feet from the summit to approach rapidly in a straight line flight about four to five feet off the ground. In one case there was no wind noticeable; in the other case, a fair breeze was blowing at right angles to the butterfly's flight. On February 13, 1967, 27 marked *P. zelicaon* males were released 2,600 feet to the north of the summit. Three of these were recaptured on the summit about a half-hour later. During this time a steady, fresh breeze was blowing from the west, presumably at right angles to their flight paths.

Pierids were easily watched in their summit approaches because of their conspicuous white color. *Pieris protodice* males were twice noted to approach the summit from the east along a ridge and once from the south slope. These flights occurred when no breeze was noticeable and when a slight breeze was present; one flew at right angles to a breeze. *Anthocaris cethura* males mostly approached the summit of Dictionary Hill from the south or southeast slopes. One male approached the summit from the east side while a wind was blowing from the northwest. On February 18 and 21, 1967, on Two Mile Hill, many *cethura* were seen to approach the summit on the south slope while fresh breezes blew from the southeast. Like *protodice*, *cethura* males approached summits over a particular, stereotyped flight pathway.

The four *Vanessa* species approached the summit of Dictionary Hill from the east and sometimes from the west. Their straight approach flight, observed from the summit, changed to circling and alighting behavior once the top was reached.

Erynnis tristis males were frequently seen at the summit in apparent approach flights from the east. Only one was seen to approach from any distance from the summit. This male was seen about 200 feet down the north slope in a steady uphill fight and became territorial on the summit one minute later.

In May of 1966 and 1967, four species were hilltopping abundantly on Dictionary Hill between 0700-0800, two hours after sunrise, when updrafts, if present, would have been slight.

In summary, approach flight by butterflies was noted both into and with winds of various strengths and at various random angles to the wind, and during times when updrafts were both maximal and minimal.

Effects of Wind at the Summit

Winds had some effect on the summit distribution of hilltopping species. Males of the four *Vanessa* species, *Papilio zelicaon*, and *Euphydryas chalcedona* were noted at times to remain on or close to the summit during fresh breezes (17-21 knots on the Beaufort Scale for wind) by flying into the wind. During these winds, hilltopping species mostly confined their activities to the leeward side. The *Vanessa* species often flew into fresh afternoon breezes blowing from the west to maintain position along the east edge of the summit. *P. zelicaon* males on Dictionary Hill often confined their hilltopping activities to the leeward side of the summit but did not buck fresh breezes to remain on the summit when the breezes were generally over the whole hill. *E. tristis* males confined their territorial activities along the east edge of the summit during west winds. Normally they spaced themselves over much of the summit.

Females of *Papilio eurymedon*, *P. zelicaon*, *Anthocaris cethura*, *Euphydryas chalcedona*, and *Speyeria callippe comstocki* flew usually quite rapidly into the winds in approaching or flying on the summit. One female *zelicaon* first arrived on the summit with the winds, but when blown from the summit it flew into the wind to return to the hilltop.

The effect of winds above the hilltop was seen when two *P. zelicaon* females were swept up high from the summit between 1130-1200 on January 15, 1967 (calm at ground level), and when a small migration of *Vanessa cardui* headed to the northeast in

the afternoon of March 30, 1966. The *cardui* flew out about 50 to 100 yards from the summit and then were carried up and out of sight; the wind was from the southwest at a steady 7 to 9 mph.

Feeding

Actual feeding on flowers by hilltopping butterflies was not often seen. Frequently species showed hilltopping activity when no flowers were available on or near the summit, such as during the fall and winter months. Perching behavior on flowers in a territory often occurred and was distinguished from feeding behavior in which the proboscis entered the flower.

Papilio zelicaon territorial males on the summit often had pollen adhering to the underside of their bodies. Eight marked male *zelicaon* captured between 1100-1400 hours had adhering pollen. These males varied from fresh to worn wing condition which suggests that feeding probably occurs throughout their life span. Occasionally males were seen feeding on flowers at the summit before resuming hilltopping behavior. One male in the early morning was seen to leave a roosting site on the summit and to feed down the east slope without exhibiting hilltopping behavior (0725, May 9, 1967). Another male (0853, April 16, 1967), the first one to show hilltopping behavior that day, sipped water while perched on a sumac leaf. One male was seen feeding on the summit as late as 1522 (May 1, 1967); no other *zelicaon* males were seen on the summit after that time on that particular day.

Presumably male *zelicaon* feed in the morning before hilltopping and probably later in the afternoon before roosting. They may also feed away from the summit during periods of the day when actively hilltopping since certain marked males were absent from the summit at times. Some feeding by hilltopping males on the summit was seen but generally no flowers were available there. Perhaps these *zelicaon* have feeding territories, as was shown to exist in a *Papilio glaucus* population in Maryland (Fales, 1959).

Virgin females of *Papilio zelicaon* occurring on the summit, including several taken *in copula*, often had pollen adhering to their bodies. Several were seen to feed on or near the summit before performing their characteristic "circling" flight on the summit. One female fed intermittently on flowers for 30 minutes on the north slope about one-quarter mile from the summit; it had an uncollapsed spermatophore in the bursa. This particular female had no pollen adhering to its body; thus individuals

taken on the summit with no pollen could still have fed. Virgin females apparently feed for a time after pupal emergence before seeking the summit to mate.

The *Vanessa* species fed extensively on flowers in the morning in home gardens surrounding Dictionary Hill, especially on lantana. At 1150 on April 13, 1966, many *Vanessa* individuals fed on yellow composites on the north slope, but none were hilltopping up to the departure time of 1310. Occasionally *Vanessa* individuals fed on or near the summit but always before starting their afternoon hilltopping behavior. One *V. caryae* male fed on the summit as early as 0725, two hours and twelve minutes after sunrise (May 2, 1967) when the temperature was 54°F. During the height of *Vanessa* hilltopping activity, individuals did not feed, although when they began to hilltop there was some overlap of feeding individuals and hilltopping individuals.

Numerous *Euphydryas chalcedona* males on the summit were sometimes seen feeding on yellow composites and at the same time displaying aggression toward each other and passers-by. One mated female was collected while feeding on the summit.

Other species noted feeding on the summit included a male and a virgin and mated female of *Anthocaris cethura*, a male and a virgin female of *Pieris protodice*, a female *Pieris rapae*, a male *Speyeria callippe comstocki*, a female *Chlosyne gabbi*, a virgin female *Leptotes marina*, a male *Callophrys dumetorum* (feeding in its territorial area), two male *Erynnis tristis*, and a male *Erynnis funeralis*.

Roosting

Crane (1967) mentions that five species of *Heliconius* in Trinidad roost gregariously, the same individuals returning to the same bushes or vines on successive nights. McFarland (1965) says that the lycaenid *Callophrys macfarlandi* roosts in clumps of *Nolina*, its foodplant. *Ministrymon leda* also roosts on its foodplant (Mesquite) in southern Arizona. Such gregarious roosting and foodplant roosting were not noticed on the summit of Dictionary Hill. Rau & Rau (1916:251-257) describe sleep postures of some butterflies and include an annotated bibliography on the subject. Roever (personal communication) says that *Vanessa* species roost in palo verde trees on the summit of "A" Mountain near Tucson, Arizona.

The vegetation on the summit of Dictionary Hill is extensive so that roost sites were difficult to locate. During April and May,

1967, eleven attempts were made to locate species roosting by inspecting the summit early in the morning and late in the afternoon. Both hilltopping and non-hilltopping individuals were found roosting. Non-hilltopping individuals included a male *Nymphalis antiopa*, two female *Euphydryas chalcedona*, and a female *Papilio zelicaon* (all three females contained spermatophores). Roosting males of hilltopping species included two *Vanessa atalanta*, one *V. cardui*, one *Speyeria callippe comstocki*, one *Euphydryas chalcedona*, and 14 *Papilio zelicaon*; these roosted mostly in weeds along the edge of the summit. The one *E. chalcedona* male and four of the *P. zelicaon* males were recaptures from previous days. One *P. zelicaon* male was recaptured roosting on three successive mornings along a 55-yard strip of weeds. On April 30 this specimen sunned itself at 0940 and was captured in hilltopping behavior at 1020. Roosting specimens were found most often in the early morning on the summit vegetation with closed wings or with wings open to sun themselves. *P. zelicaon* males when disturbed from sunning positions flew quite rapidly and alighted again on vegetation almost immediately.

Many hilltopping species of flies were noted roosting on the summit on Broom Baccharis. Catts (1963) found that at least some *Cuterebra latifrons* (Cuterebridae) males spent the night in chaparral on a hill summit and resumed territorial behavior on the summit at temperatures of about 19° C. Catts (1964), working with the oestrid flies *Cephenemyia apicata* and *C. jellisoni*, mentions that males roosted in and near hilltop aggregation sites.

Predation

Knudsen (1954) reported several hundred butterflies of three hilltopping species in an area of a few hundred square feet on the summit of Kennesaw Mountain, Georgia, and Waterhouse (1932) collected over 300 butterflies of three species on top of Kosciusko in Australia in one day. About 25 to 100 butterflies are usually encountered on a given day during late February, March, and April on the summit of Dictionary Hill. Concentrated predation on such large numbers of butterflies was expected but not seen. *Vespula* wasps have been known to prey on a hilltop swarm of winged ants (Chapman, 1963), and there is a report of sparrows attacking a "mud-puddle club" of *Papilio glaucus canadensis* (Rawson & Bellinger, 1953), but no such attacks were observed during this study.

Predators reported attacking adult butterflies include the following: robber flies (Fryer, 1913; Dover, 1920; Field, 1938; Klots, 1951; Price, 1961), dragonflies (Scudder, 1889; Fryer, 1913; Dover, 1920; Field, 1938; Klots, 1951; Price, 1961), Hymenoptera (Scudder, 1889; Ford, 1957), Hemiptera (Field, 1938; Macy & Shepard, 1941; Klots, 1951), mantids (Field, 1938), crab spiders (Field, 1938; Klots, 1951; Voss, 1953), web weaver spiders (Klots, 1951), frogs (Klots, 1951; Price, 1961), toads (Klots, 1951), lizards (Dover, 1920; Annandale & Dover, 1921; Field, 1938; Klots, 1951; Ford, 1957), tree-snakes (Dover, 1920; Annandale & Dover, 1921), many different birds (Scudder, 1889: 1612; Fryer, 1913; Dover, 1920; Annandale & Dover, 1921; Carpenter, 1937, 1941a,b; Field, 1938; Klots, 1951; Knowlton, 1953; Ford, 1957; Urquhart, 1960:209; Olson, 1962; Petersen, 1964), bats (Field, 1938), chipmunks (Morris, 1953), and monkeys (Field, 1938; Klots, 1951).

During this study no butterfly predation was seen. However, certain potential predators such as lizards and birds were occasionally present on the summit of Dictionary Hill. Also, territorial male butterflies often had beak-marks or "beak injuries" from birds (see Carpenter, 1937), although such predation attempts may have occurred away from the summit.

A flycatcher (*Myiarchus cinerascens*) was sighted on eight different days over a 25-day period (presumably the same individual). The bird perched for extended periods and frequently darted out after passing insects. A whippoorwill (*Chordeiles* sp.) was sighted on the summit one late afternoon for one-half hour and one morning briefly. Swift lizards and horn-toad lizards were occasionally present. Crab spiders (*Misumenoides formosipes*, determined by B. Kaston) were present on the summit in curled sumac leaves in late September, 1967, and were not present in sumac bushes checked below the summit. Some of these spiders fed on hilltopping flies. Conceivably these spiders might also eat butterflies that perch on the sumac leaves, such as *Vanessa virginiensis* and *Strymon melinus*.

DISCUSSION

In this section a number of topics will be discussed in relation to hilltopping behavior in butterflies. The probable function of hilltopping in butterflies as a means of congregation to facilitate mating will be advanced, and other methods that butterflies may use to congregate for mating will be pointed out, along with some discussion of the courtship devices used. The func-

tion of territoriality in relation to hilltopping will be developed, and comparisons will be drawn between hilltopping insects and hilltopping butterflies. Special attention will be given to wind and updrafts in relation to hilltopping. In addition, possible methods of orientation in approaching summits and the extent to which hilltopping has developed in butterflies will be described.

Shepard (1966) defined a "hilltopping" butterfly as a "species which is found on a hilltop in only one stage of development [adult]; the food source of the larvae is not present; the insects are not forced there by a macro-environmental factor such as strong winds." In light of the results of the present study, this definition should be modified: "*Hilltopping* in butterflies is a phenomenon in which males and virgin or multiple-mating females instinctively seek a topographic summit to mate. The generalized behavior pattern of hilltopping species is given in Fig. 15. Hilltopping apparently *does* occur in some species whose larval foodplants are present on or near a summit as well in species that fly to a summit a considerable distance away from the nearest foodplant. Territorial or patrol behavior at the summit is the most conspicuous aspect of the hilltopping male butterfly.

The idea that hilltopping butterflies congregate on summits for the purpose of mating is mentioned occasionally in the literature. Seitz (1909) said that the sexes in *Papilio machaon* and *P. podalirius* meet on summits for mating but did not cite supporting evidence. Moffat (1922) suspected that *Vanessa cardui* and *V. atalanta* individuals on a hilltop at Wexford, Ireland, were males; each "attacked" all newcomers "to keep the ground to himself in the hope that ultimately a female would appear." Moffat also thought that hilltopping was a peculiarity of the mating season since during a different time of the year *Vanessa* individuals were in lowlands but not on summits, while neither species was seen in the lowlands when hilltopping. (However, *V. cardui* and *V. atalanta* hilltop only in the afternoons, so that this observation was probably a reflection of the time of day rather than the time of year.) Peile (1923) noted that *Melitaea trivia persea* males in Mesopotamia frequent ridge crests; he found one pair *in copula* on a crest and concluded that ridge crests are probably their mating sites, "the males waiting there to waylay the females as they come by." Clark (1932:192) mentioned that *Papilio polyxenes asterius* mates on summits but gave no details. Temple (1953) reported that *Pararge megaera* mated after "all moved uphill to a stony arid place." Wyatt (1957a)

found two *in copula* pairs of *Papilio machaon aliaska* on a ridge summit where hilltopping males were active. Guppy (1962) concluded from observations on *Oeneis nevadensis* that hilltopping serves to bring the sexes together. He did not report any actual matings. Guppy developed certain theoretical implications of this mechanism. He pointed out that hilltopping is probably an instinct to fly to a central point in newly emerged individuals; females would lose this instinct once mated and would depart to oviposit. Natural selection would eradicate the habit if no mating occurred. An important point to stress that Guppy mentions is that females would be on summits only for the brief time to mate and thus a collector could easily miss seeing them. Emmel and Emmel (1967) reported that *Papilio indra kaibabensis* males "hilltop" on the rims of the Grand Canyon, Arizona, where presumably virgin females fly up to mate, several thousand feet higher than their nearest foodplants.

Other methods for bringing the sexes together for mating besides hilltopping probably include males flying to treetops; over rockslides; through bogs; in canyons, stream courses, and gullies; and around the larval foodplant. Jackson (1961) suspected that members of the lycaenid subgroup Lipteninae in Uganda ascend to treetops to mate since most of the females collected there had fresh wing condition. Examples of each type are given in Table 22. It remains for future investigation to establish the importance of these methods for mating in butterflies.

Catts, Garcia, and Poorbaugh (1965) found that males of the oestrid fly *Hypoderma lineatum* aggregate probably for mating along the open margins of streams in pastureland ravines. Certain other members of this family mate at summit congregation sites. Mating of *Sirex noctilio*, a siricid wasp, occurs on treetops where males periodically swarm (Morgan, 1968). Certain other species in this family are known to "hilltop." In moths certain members of the Lasiocampidae, Bombycidae, Saturniidae, and Arctiidae mate by the males homing in, sometimes over long distances, on a pheromone that the virgin female releases (Butler, 1967; Ewing and Manning, 1967). No such long-range method has been noted for butterflies. Certain butterfly congregations probably serve no mating function, such as male congregations for feeding (Reinthal, 1966) and butterfly migrations (Williams, 1930).

If hilltopping is a mating mechanism in insects, one would expect this behavior pattern to be developed to a greater extent

TABLE 22. Probable methods of bringing sexes together for mating in butterflies besides hilltopping

Method	Examples
1. Tree-top seeking	<u>Delias</u> spp. (Seitz, 1927:123), <u>Eriboea</u> spp., <u>Charaxes</u> spp., <u>Euripus consimilis</u> , <u>Euthalia</u> <u>garuda</u> (last four from Wynter- Blyth, 1957).
2. Rock-slide fliers	<u>Erebia magdalena</u> , <u>Chlosyne</u> <u>damoetas</u> , <u>Lycaena snowi</u> , <u>L. hypophlaeas</u> .
3. Confined to bogs	<u>Colias scudderi</u> , <u>Oeneis jutta</u> (Klots, 1951), <u>Boloria eunomia</u> (Klots, 1951), <u>Speyeria</u> <u>nokomis</u> , <u>Incisalia lanoraieen-</u> <u>sis</u> (Klots, 1951).
4. Canyon, gully, and stream fliers	
a. Territorial species	<u>Asterocampa celtis</u> , <u>Chlosyne</u> <u>gabbi</u> , <u>Euphydryas chalcedona</u> ssp., <u>Junonia coenia</u> , <u>Limenitis</u> ssp., <u>Lycaena hermes</u> , <u>Apodemia</u> <u>mormo</u> ssp., <u>Lephelisca wrightii</u> .
b. Patrollers	<u>Papilio eurymedon</u> , <u>P. multi-</u> <u>caudata</u> , <u>P. rutulus</u> , <u>Anthocaris</u> <u>lanceolata</u> , <u>A. sara</u> , <u>Pieris</u> <u>beckerii</u> , <u>Philotes sonorensis</u> .
5. Confined to larval foodplants (recognition of foodplant by males)	<u>Neophasia menapia</u> , <u>N. terlooti</u> , <u>Adelpha bredowii</u> , <u>Brephidium</u> <u>exilis</u> , <u>Philotes</u> spp., <u>Plebejus</u> <u>icarioides</u> , <u>Habrodais grunus</u> , <u>Hypaurotis crysalus</u> , <u>Mitoura</u> <u>gryneus</u> , <u>M. loki</u> , <u>M. siva</u> , <u>Satyrrium dryope</u> , <u>S. sylvinus</u> , <u>Ochlodes yuma</u> , <u>Pseudocopaodes</u> <u>eunus</u> .

Examples from personal experience except where otherwise noted.

in groups that are rare, parasitic, predaceous on ephemeral prey, or whose larval foodplants are scattered or rare than in common species or species that mate at the larval foodplant. Such groups are more likely to need a common meeting ground to facilitate mating. The following evidence supports this hypothesis.

1. Chapman (1954a) concludes from an insect survey of the summit of Squaw Peak in Montana that "parasitic and not usually abundant groups of insects were well represented."

2. Dodge and Seago (1954) report that flies collected by net on Georgia summits produced many undescribed or little-known species for which the females and life histories of most were unknown. Their entire net-collected Sarcophagidae represented more than 16 saprophagous species and more than 36 parasitic species.

3. Hilltop congregations are reported for all the major groups of parasitic bot flies (Catts, 1964): Cuterebridae, Gastrophilidae, Hypodermatidae, and Oestridae. Grunin (1959) points out that large concentrations of male bot flies on summits indicate the scarcity or absence of males in the surrounding territory and since bot flies generally have scattered, low density populations, these gathering points are probably mating places. A number of matings of bot flies on summits has been reported by Catts (1963, 1964).

4. Hagen (1962) summarizes the characteristics that aggregating Coccinellidae beetle species have in common; most of these congregate on some prominent object that forms a silhouette on the horizon, including peaks and hills. The species that aggregate are associated with "ephemeral" prey, chiefly aphids, and not with sessile Homoptera. Four large tribes which do not have many species that aggregate feed mostly on scale insects, mealybugs, or fungi—all sessile prey. Species that *do* aggregate in these tribes have ephemeral prey. Aphid-feeding species of Coccinellini that do not form aggregations feed mostly on colonial, arboreal, non-migrating aphids. Hagen suggests that "ephemeral" food led to the selection for long dormancy in the absence of food and for aggregation to bring the dispersed sexes together. Mating occurs mostly at these aggregation sites before the beetles disperse at the end of dormancy.

5. There is some evidence to show that rarer species of butterflies are more likely to hilltop than abundant species. J. Scott (in manuscript) collected butterflies randomly in Gregory Canyon, Boulder County, Colorado, from March to May, 1966, to see if species present that are known to hilltop were rarer than

non-hilltopping species. Using number of individuals collected per hour as an index, he found for 32 hilltopping species and 34 non-hilltopping species that hilltopping species averaged a third as abundant as non-hilltopping species. Although there was considerable overlap in the amount of abundance, the upper and lower ends of the scale differed significantly:

	Number of non-hilltopping species	Number of hilltopping species
One or more per hour	10	3
One-fourth or less per hour	11	21

Of the three most abundant hilltopping species, *Polites themistocles* and *Incisalia eryphon* apparently are only weak hilltoppers, and *Celastrina argiolus cinerea* may not hilltop as evidenced by the high percentage of mated females (see Table 15) collected by Scott, although *C. a. echo* definitely does hilltop in southern California.

Another advantage of hilltopping besides the congregation of adults that occur in low numbers or are scattered is the development of a stabilized gene pool from the centralization of isolated populations during mating (Catts, 1963).

Wind and updrafts as causative agents for hilltopping in butterflies seem unlikely for the following reasons. Some butterflies approach summits into the wind or at random angles to the wind, as well as flying with the wind. Butterflies actively seek and stay on hilltops during windless days, sometimes before updrafts would have much effect. Butterflies maintain a position on or near the summit even during fresh breezes. *Euchloe olympia* (Arnhold, 1952) and *Boloria polaris gronlandica* (Munroe, 1951) have been noted to return to summits after being blown off the tops by winds. Butterflies that are non-hilltoppers fly up-and-over the summit and show no such "staying" behavior. *Vanessa* species hilltop in the afternoons when winds would have much more effect than updrafts; these species often approached the summit into the wind as well as with the wind.

Shepard (1966) noted the behavior of hilltopping *Pieris occidentalis* males in relation to winds on Slate Peak, Washington. No specimens were seen approaching the top from the west where winds blow directly up out of the valleys. All arrived from the east slopes where winds were limited until the summit

was reached. They had to fly against the wind to reach the very summit.

Glick (1965) states that certain species of butterflies are wind-propelled by their manner of flight when flying directly into a strong wind. They keep their wings vertical and open and close them alternately to offer the least wind resistance. The butterfly is driven forward by the wind eddying against the wing under-surface.

Winds and updrafts in relation to other hilltopping insects parallel the findings with butterflies. Chapman (1954a) found on Squaw Peak, Montana, that "early morning summit activity was frequently considerable by 8:00 a.m. when updraft currents would be expected to be slight if present at all." Dodge and Seago (1954) noted summit activity of flies during moderate to strong winds. Aldrich (1915) reported that hovering bot flies actively maintain themselves on summits during strong breezes. Hurd (1920) mentioned that some beetles were carried by ascending winds and precipitated on a summit against their flight powers. However, Edwards (1956, 1957a) suggests that winds do not draw Coccinellidae beetles to summits. He mentions that they sometimes fly to and stay on summits on windless days as well as flying against the wind in approaching summits.

Chapman (1954b) noted in detail the effects of winds on the summit behavior of winged ants on Squaw Peak, Montana. Maximum numbers of ants were present on warm, calm days when updrafts would have their greatest effect. Sometimes the ants had difficulty maintaining themselves on the summit against the wind but were not noted to swarm in calm eddies present just below the summit. He states that air currents may play a role in transporting ants to summits but are not entirely responsible for summit swarms of ants. The evidence for this is that (1) ant swarms are localized to the actual summits and are not present along approaches where wind eddies exist, (2) lookout stations reporting "tens of thousands" of ants included grassy or brush and forest covered ridges and hills where thermal updrafts are not well developed, and (3) updrafts strong enough to be a transportation factor would carry ants up and away from summits.

In his study of Squaw Peak summit insects, Chapman (1954a) listed the following reasons why updrafts do not account for the presence of all insects on summits: (1) updrafts would not be symmetrical enough to concentrate insects over a peak as opposed to slightly lower points, (2) updrafts may carry insects

up and away from the peak, (3) updrafts are unlikely to be so selective for species and sex, and (4) updrafts would not account for "the continued presence of the large strong and fast fliers" which could easily leave the peak at any time.

Mani (1962) distinguished between insects actively seeking summits and insects passively transported by wind in the Himalayas. Vertical convection currents lift many insects including heavy-bodied forms up from the plains, where they are transported by upper-air winds, chilled, and dropped on snow and glaciers. Winged insects alive on summits are visitors from other biota lower down and have been observed ascending even when no updrafts are present and sometimes against prevailing winds, according to Mani.

Thermal updrafts on mountains are discussed by Malone (1951:663), Chapman (1954b), and Geiger (1965:407-408). Updrafts are most noticeable on southern slopes and are negligible on northern slopes. They are clearly defined on warm calm days. They are strongest at 20 to 40 meters above the ground where they average two to four meters per second. Updrafts are strongest in canyons and gullies and are weak on projecting ridges. In the northern Rocky Mountain region, updrafts generally start about 9:00 a.m. and continue to late afternoon. Updrafts reach their greatest intensity at one-and-one-half to two hours after maximum insolation.

Orientation flight toward the summit by both sexes in butterflies is almost certainly visually directed. Release experiments with *Papilio zelicaon* males on Dictionary Hill suggest that they can "home in" on the summit when released at various distances and directions and in various wind directions and velocities. Given a choice, male *zelicaon* could discriminate between which hilltop they were collected from and some other hilltop. When male *zelicaon* were released at considerable distances away from the hilltop, one could predict which new hilltop in the vicinity they would seek. Female *zelicaon* are probably responding like the males in seeking a summit and are not brought there by random flight because of the large numbers that are virgin and because only virgins sought the summit in a release experiment with mated and unmated females.

Certain insects are known to orient to distant objects (silhouettes) on the horizon. Iersel and Assem (1965) found that females of the wasp *Bembix rostrata* return to their nests by orienting to tree tops as far as 80 meters away on the horizon. Schneider (1962) reports that the beetle *Melolontha vulgaris*

after hibernation selects the area on the horizon with the greatest average height (hypotaxis) within a radius of about 3.2 kilometers during a spiral flight. Once the area is located, the beetles maintain a steady flight to the area, which is a forest or hill. Presumably a similar type of orientation and directional flight exists for males and virgin or multiple-mating females in hilltopping insects.

Kennedy (1939), investigating the upwind flight of the mosquito *Aedes aegypti*, found that the mosquitos maintained upwind flight orientation by visually referring to the apparent movement of the ground. In hilltopping insects, a combination of visual orientation to the ground and to the horizon would seem necessary to approach summits.

Once the summit is reached, the hilltopping butterfly begins territorial or patrolling behavior. In essence, the whole summit can be considered a macro-territory for the butterflies present, with micro-territories and patrol pathways established within this territory. Beusekom (1948) found that the female wasp *Philanthus triangulum* perceives micro-topographic landmarks in finding the nest, a behavior learned during one or more orientation flights. A similar learning process probably takes place in butterflies that establish territories on summits.

Nobel's (1939) definition of territory as "any defended area" has been applied to a wide variety of animals. Alexander (1961) points out that two phenomena are widely associated with territorial animals: (1) a tendency to stay in restricted areas, or to repeatedly return to specific areas, or both; and (2) aggressive behavior displayed toward intruding individuals. Carpenter (1958) reviewed territoriality in vertebrates — it is exhibited by fish, amphibians, reptiles, birds, and mammals. A general discussion of territoriality as it applies to insects is given by Alexander (1961:172-174) and Catts (1963:83-84). Catts (1963) states three criteria for proving the existence of territoriality in tagged male Diptera on summits: (1) the stationing of marked males at summits, (2) frequent intraspecific encounters with intruding males, and (3) diurnal permanence of male stations within a specific area. Presumably conditioning by familiarity with the microenvironment allows the male to dominate in his territory (Nice, 1941; Hinde, 1956). Possible advantages due to the spacing of a congregated, territorial male population include: (1) decreased chances of mass predation by a few predators, (2) less time spent in intraspecific aggression, (3) in-

creased frequency of male-female encounters, and (4) decreased interference to courting and mating pairs by other males (Catts, 1963; Lin, 1963). Catts (1963:83) emphasizes the need to observe marked individuals before territoriality can be shown to exist in a species.

Territorial behavior has been proven by mark-recapture methods for certain insect species. In Diptera territoriality is exhibited by the families Cuterebridae (Catts, 1963) and Oestridae (Catts, 1964). In Hymenoptera it is exhibited by Megachilidae (Jaycox, 1967) and Sphecidae (Lin, 1963). In Odonata territoriality is exhibited by certain dragonflies (Jacobs, 1955; Ito, 1960; Kormondy, 1961; Johnson, 1962b, c; Moore, 1964) and damselflies (Bick and Bick, 1963). In Orthoptera it is exhibited by Gryllidae (Alexander, 1961).

Strong circumstantial evidence for territoriality (a perch area combined with aggressive behavior in males) also exists for the following insect groups: Diptera in the families Gastrophilidae (Grunin, 1959) and Hypodermatidae (Grunin, 1959); Hymenoptera in Andrenidae (Linsley, 1958; Cazier & Linsley, 1963), Apidae (Janzen, 1964; Bennett, 1966; Cruden, 1966), and Scelionidae (Wilson, 1961); Coleoptera in the genus *Necrophorus* (Pukowski, 1933); and Odonata in dragonflies (Moore, 1952; Johnson, 1962a, 1964; Pajunen, 1962; Young, 1965) and damselflies (Bick & Bick, 1965; Bick & Sulzbach, 1966).

Strong circumstantial evidence exists for territoriality in various Lepidoptera species as well (Table 23). Ross (1963) marked males of two species of *Hamadryas* in an effort to prove or disprove territoriality in these species and found that they did not frequent definite perch areas but did display aggression. Pugnacity is known in a large number of butterfly species. Shapiro (1966) reported pugnacious males for one papilionid, two pierids, seven nymphalids, four lycaenids, and 18 hesperiid species in Delaware Valley, Pennsylvania.

Characteristically, aggressiveness, or pugnacity, of territorial male insects can be divided into four parts: (1) investigation flight toward intruders into the male's territory, followed by (2) chase of the intruder, or (3) intraspecific fight, or (4) a return to the perch area (Lin, 1963; MacNeill, 1964). Generally the male is perched, or resting, at a perch site in his territory until he investigates passing intruders (MacNeill, 1964). However, some species "patrol" a territory (e.g., the butterflies *Papilio thersites*, *Battus philenor*, *Anthocaris cethura*) and perch briefly

TABLE 23. Butterfly species that have territorial behavior, presumed from circumstantial evidence
(perch area or site combined with aggressive behavior)

Species	Sources
PAPILIONIDAE	
<u>Chilasa clytia</u>	Wynter-Blyth, 1957
<u>Papilio thersites</u>	Shoumatoff, 1953
NYMPHALIDAE	
<u>Apatura iris</u>	Richards, 1927:304
<u>Charaxes species</u>	Van Someren, 1955; Wynter-Blyth, 1957
<u>Eriboea species</u>	Wynter-Blyth, 1957
<u>Hypolimnys misippus</u>	Stride, 1956
<u>Lethe creola</u>	Klots, 1951
<u>L. portlandia</u>	Klots, 1951
<u>Limenitis astryanax</u>	Shapiro, 1966
<u>Nymphalis antiopa</u>	Hargitt, 1915; Clark, 1937; Shapiro, 1966
<u>Oeneis nevadensis</u>	Guppy, 1962
<u>Phyciodes tharos</u>	Klots, 1951
<u>Polygonia comma</u>	Tietz, 1952
<u>Vanessa gonerilla</u>	Hudson, 1898
<u>V. itea</u>	Hudson, 1898
LYCAENIDAE	
<u>Lycaena phlaeas americana</u>	Klots, 1951
<u>Satyrium titus</u>	Shapiro, 1966
HERPERIIDAE	
<u>Abantis paradisea</u>	Van Someren, 1955
<u>A. tettensis</u>	Van Someren, 1955
<u>Agathymus evansi</u>	Roever, 1964
<u>Atrytonopsis hianna</u>	Shapiro, 1965
<u>Bibasis sena</u>	Wynter-Blyth, 1957
<u>Coeliades forestans</u>	Van Someren, 1955
<u>Epargyreus clarus</u>	Saunders, 1932
<u>Hesperia species</u>	MacNeill, 1964
<u>Hesperia metea</u>	Shapiro, 1965
<u>Pyrgus communis</u>	Clark, 1937
<u>Thorybes pylades</u>	Klots, 1951

if at all. Presumably the perched individual is conserving energy between aggressive encounters. MacNeill (1964:24) divided intruder-insects investigated by *Hesperia* into three categories on the basis of male behavior: (1) insects not of the same or a closely related species, (2) females of the same or a closely related species, and (3) males of the same or a closely related species. He found that male *Hesperia* will often investigate other butterflies and insects but would chase and fight only with males of the same or closely related species.

The primary function of territoriality in insects seems to be to increase the probability of mating (Alexander, 1961; Kormondy, 1961; Wilson, 1961; Johnson, 1962b; Catts, 1963, 1964; Cazier & Linsley, 1963; Lin, 1963; Johnson, 1964). Increased mating probability was the selective force necessary for "the origin and maintenance of territoriality" in dragonflies (Johnson, 1962b). Alexander (1961) found that territoriality in field crickets appeared in low density populations and was absent in high density populations, with both conditions producing a maximum degree of insemination of females.

Movement is necessary to elicit the courtship approach in all male butterflies that have been investigated (Marler and Hamilton, 1967:258). Some work has been done to isolate the stimuli that males are responding to. Tinbergen (1965) tested the Grayling, *Eumenis semele*, and found that bigness, darkness, nearness, and dancing activity of the moving object stimulated the male to respond. Swihart (1967) found that certain butterflies respond maximally to colors most like their wing pigmentation. In the nymphalid *Hypolimnas misippus*, the early stages of courtship are visually controlled and the later stages are probably "behavioral" and chemosensory (Stride, 1956, 1957, 1958).

Pheromones emitted by androconia hairs and scales are used by many male butterflies to stimulate the female during courtship. Families containing species with pheromones include Papilionidae, Pieridae, Nymphalidae, Lycaenidae, and Hesperidae (Clark, 1927; Ford, 1957). The male odors are often perceptible to man, but the female "directive" odors are not and their presence is inferred from behavior (Ford, 1957).

Once the female is mated, certain barriers to further insemination may develop. Labine (1964) found that there may be a female "awareness" of the presence of a spermatophore that makes her resistant to courting males. In the butterfly genera

Parnassius, *Euphydryas*, *Speyeria*, and *Acraea*, the male secretes a plug (sphragis) on the female during copulation that helps prevent further mating (Labine, 1964). In the moth *Atteva punctella*, the presence of a spermatophore does not initiate oviposition but seems responsible for an inhibition of receptivity to males (Taylor, 1967). Various authors have noted that an ascending flight by mated females of certain species is an avoidance behavior to male courtship (e.g., Stride, 1958).

Table 2 lists species that are known to hilltop. Those species reported by Scudder (1887, 1889) and Weiss (1927, 1928) were merely listed as present on summits and thus need to be verified. The genus and species names listed were brought up to date with current nomenclature where known.

Certain genera in North America are apparently devoid of hilltopping species (list not exhaustive): *Colias*, *Cercyonis*, *Erebia*, *Phyciodes* (one possible exception), *Apodemia*, *Lephelisca*, *Lycaena*, *Philotes*, *Plebejus*, *Ochlodes*, *Pholisora*, *Pyrgus*, *Agathymus*, and *Megathymus*. K. Brown (in letter) says that certain members of the genus *Doxocopa* strongly hilltop in the early afternoons in Brazil. *Doxocopa* is probably congeneric with *Asterocampa*, although no members of *Asterocampa* apparently hilltop in Brazil or North America.

Table 24 lists eight North American genera that contain many hilltopping species. The genera *Erynnis* and *Hesperia* probably contain additional hilltopping species as yet unrecorded. Hilltopping genera containing certain species that weakly hilltop include *Speyeria* (except *callippe* and *egleis*), *Boloria* (except *astarte*), *Limenitis*, and *Incisalia*.

Ten of the eleven species of *Vanessa* (= *Pyrameis*) in the world are reported to hilltop (see Table 2). Only the species *samani* has not as yet been reported to hilltop. *V. cardui* is reported to hilltop in all the realms of the world except as yet in the Neotropical.

Hilltopping is widespread in butterflies both geographically and taxonomically. Representative species are present in all the geographic realms of the world (see Table 2). Tropical regions have large numbers of species which hilltop (see Van Someren, 1955; Brown, Table 2), although little work has been done to catalogue and study these. Sixteen of the 25 subfamilies of butterflies and five of the six families contain species which hilltop (Table 25). Of the nine subfamilies that are, at present, not known to hilltop, four (Baroniinae, Pseudopontiinae, Calinaginae, and Styginae) contain only one species each and the

TABLE 24. Genera from North America north of Mexico that contain many hilltopping species

Genus	Total number species	Number species known to hilltop	0/0 that are hilltopping species	Source of total species number
<u>Papilio</u>	15	11	73.3	Ehrlich and Ehrlich, 1961
<u>Euchloe</u>	3	3	100.0	"
<u>Oeneis</u>	10	5	50.0	"
<u>Euphydryas</u>	6	3	50.0	"
<u>Vanessa</u>	4	4	100.0	"
<u>Erynnis</u>	17	11	64.7	Burns, 1964
<u>Hesperia</u>	18	12	66.7	MacNeill, 1964
<u>Thorybes</u>	6	4	66.7	dos Passos, 1964

Papilio species from extreme southern Florida and southern Texas and strays were not considered. Also, P. nitra is here considered a hybrid form.

TABLE 25. Butterfly subfamilies in which species
are known to "hilltop" *₁

PAPILIONIDAE
Baroniinae
Parnassiinae
* Papilioninae
PIERIDAE
* Coliadinae
* Pierinae
Dismorphiinae
Pseudopontiinae
NYMPHALIDAE
Ithomiinae
* Danainae
* Satyrinae
* Morphinae
* Charaxinae
Calinaginae
* Nymphalinae
* Acraeinae
LIBYTHEIDAE
Libytheinae
LYCAENIDAE
* Riodininae
Styginae
* Lycaeninae
HESPERIIDAE
Megathyminae
* Coeliadinae
* Pyrrhopyginae
* Trapezitinae
* Pyrginae
* Hesperinae

₁ This subfamily classification for true butterflies (Papilionidae through Lycaenidae) follows Ehrlich (1958) and Ehrlich and Ehrlich (1967) and for skippers (Hesperiidae) follows Brues, Melander, and Carpenter (1954).

subfamily Libytheinae contains only ten species. Of the four remaining subfamilies that are not known to hilltop, Megathyminae fairly certainly does not (Roever, pers. comm.) and Parnassiinae, Dismorphiinae, and Ithomiinae have so far not been reported to do so.

The fact that most subfamilies contain species which hilltop and certain genera contain species which do strongly while other genera have species which do not or only weakly suggests that the hilltopping instinct has very likely developed independently in various groups at various times.

CONCLUSIONS

Hilltopping in butterflies is so widespread that it must serve an essential function and have survival value. This study offers the following evidence that this phenomenon serves to bring males and females together to insure fertilization and that other explanations for this behavior lack validity.

1. From many sources it is apparent that males of hilltopping species occur in far greater numbers on the summits of favorable hills than they do in the surrounding areas; therefore, some mechanism is operating to create relatively high densities of male populations, with some degree of stability, in very limited areas.

2. The summits offer little to attract the males that they could not find elsewhere in the way of nectar sources, moisture, larval foodplants around which the females might be emerging, shelter, and warmth.

3. Males on summits adopt territorial behavior including "patrolling" and aggression which are sexually oriented behavior patterns.

4. Females, however, do not remain on the summits unless they are unmated and males are absent or few in numbers. An abnormally high percentage of females captured on summits are virgin when compared to those captured elsewhere.

5. A substantial number of actual courtships and matings have been observed for two species on the summit.

6. Unmated *Papilio zelicaon* females, when released below the summit of Dictionary Hill, flew to the summit while mated females did not.

7. Male *P. zelicaon* released at various distances and directions from the hill were recaptured on the summit in such numbers that they must have "homed in."

A summary of the behavior patterns of hilltopping butterflies is given in Figure 15.

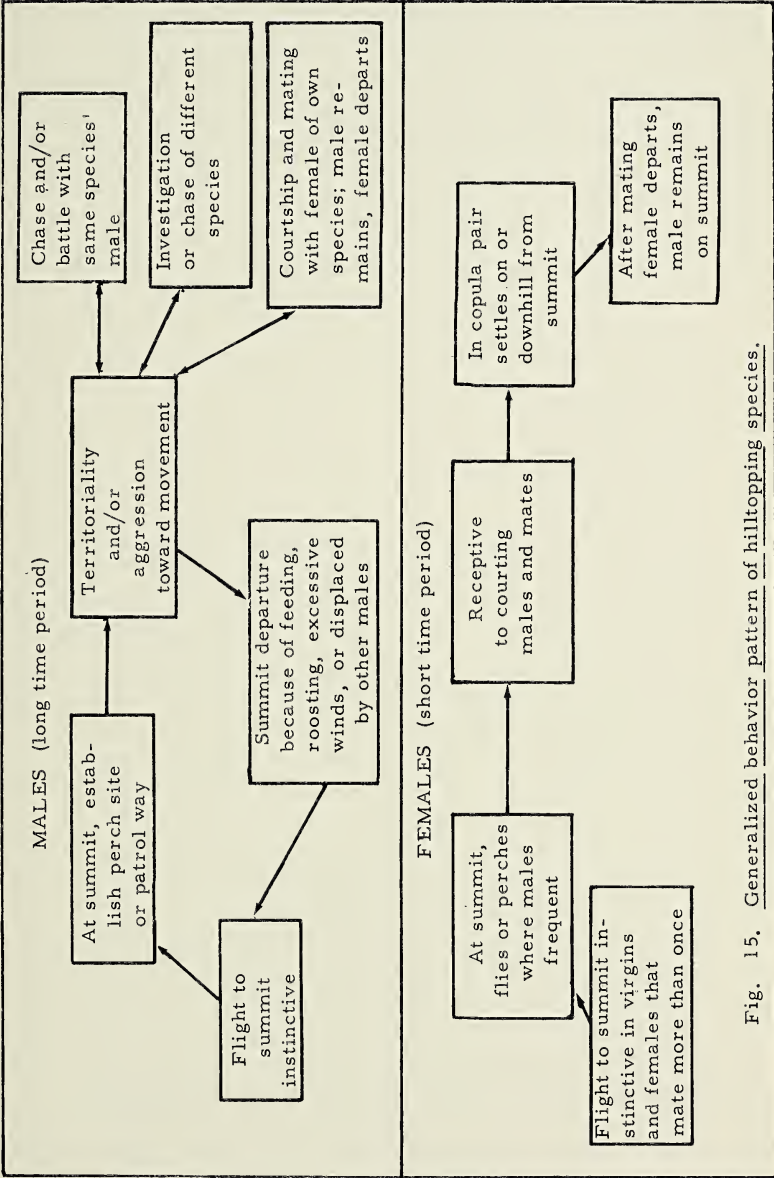


Fig. 15. Generalized behavior pattern of hilltopping species.

The urge to ascend, ascending for assembling, tropisms, and hilltops as male playgrounds, sporting grounds, or battlegrounds can be incorporated into the broader explanation of congregation for mating. However, other possible reasons given as to why butterflies congregate at hilltops do not adequately explain the phenomenon. A male surplus on summits is a misconception since hilltops are sometimes the only place that males of certain species can be collected. Attraction to summits because of a larval foodplant availability is not always true since some species ascend far away from their foodplant area. Winds and updrafts transporting butterflies to summits is unlikely since certain species remain on summits and others fly over, since some individuals hilltop on windless days and before updrafts would have much effect, and since it is unlikely that winds and updrafts are so selective for species and sex. Wind at summits as an enticement is unlikely since species hilltop on calm days more so than on windy days.

There is much information yet to be acquired by studying hilltopping butterflies.

1. Summits are excellent places to study courtship and mating behavior of species.

2. The carrying capacity in supporting a hilltopping population needs investigation. Dethier and MacArthur (1964) demonstrated that a carrying capacity exists in the butterfly *Melitaea harrisii* by introducing a large number of larvae into a field in Maine. This effect on a summit might be tested by releasing large numbers of hilltopping butterflies in an area where they would be drawn to a hilltop.

3. The possibility that there may be a selection in territorial species for males more favorable to the species should be explored.

4. More information is needed on the apparently mild predation pressure on summits and the possibility that summit roosts offer protection from nocturnal predators.

5. Additional studies are needed to substantiate how general the phenomenon of hilltopping is on a worldwide basis.

6. The stimuli which prompt butterflies to seek summits need to be determined.

7. More work is needed in correlating rare species and species whose foodplants are widely scattered with hilltopping.

8. Further studies are indicated in the interaction between the sexes in other situations besides summits, such as males seeking tree-tops, rock-slides, bogs, canyon and gully bottoms and stream courses, and by male recognition of larval foodplants.

9. The impact of migrant species on resident hilltopping species needs to be investigated.

10. The correlation between a high percentage of virginity (i.e., lack of spermatophores in females) and hilltopping behavior should be further investigated in species in the orders suspected of this behavior.¹

¹ All Lepidoptera, Hymenoptera, and certain Coleoptera families form spermatophores during mating although no Diptera do (Davey, 1960).

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IN THIS ISSUE

HILLTOPPING

AN ECOLOGICAL STUDY OF
SUMMIT CONGREGATION BEHAVIOR
OF BUTTERFLIES ON A
SOUTHERN CALIFORNIA HILL

OAKLEY SHIELDS

*Department of Biology
San Diego State College
San Diego, Calif.*

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Volume 6

Number 3

September, 1967

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Established in 1962

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA has now nearly completed six volumes. At the moment, the publication schedule is somewhat delayed due to an editorial mishap which has had no lasting effects and every effort is being made to bring publication up to the normal schedule.

An editorial team of Associate Editors is in the process of being organized to aid the general editor in the procuring and screening of manuscripts for the journal. It is hoped that we will have this team organized in time for the issuance of Volume 7 to appear shortly. In any event, such a team as will begin to function shortly will be subject to addition from time to time so that the journal will not only be representative of all branches of Lepidopterology but also all parts of the world. The general editor will be grateful to all for recommendations and comments from others.

The editor has from time to time been confronted with inquiries from readers of the journal concerning the desirability of organization of local meetings of Lepidopterists connected in some way with the Foundation. The Editor would appreciate the reaction of readers to this subject. It should be borne in mind that the Editor would not have the time to organize these local meetings but would be willing to aid their existence in any way possible, as he has done several times in the past.

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THE ORIGIN OF AUTUMNAL "FALSE BROODS" IN COMMON PIERID BUTTERFLIES

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Limnology, Cornell University,
Ithaca, N.Y. 14850*

"False broods" of common Pierid butterflies have received frequent comment in the literature (Clark 1932, Clark & Clark 1951, Rawson 1945, Shapiro 1962, 65, 66). Shapiro (1962) speculated that November and December emergence of *Colias eurytheme* Boisduval at Philadelphia, Pennsylvania resulted from premature development of pupae which would have overwintered under normal circumstances. It was suggested that such pupae had developed nearly to the point of eclosion before being arrested by the onset of cold weather. A subsequent mild spell of sufficient duration would allow them to resume their development and eclose as a late autumn "false brood." Circumstantial evidence to this effect was presented in a later note (Shapiro 1965). The present paper demonstrates that successful eclosion occurs after prolonged thermal arrest of development, and that unfed adult *Colias* are capable of prolonged survival at sustained low temperatures. Similar phenomena are reported for non-diapausing pupae of *Pieris rapae* Linnaeus and *P. protodice* Boisduval and LeConte, and their respective adults.

COLIAS EURYTHEME

"False broods" have been reported for this butterfly in a variety of localities (various authors *in litt.*). The phenomenon is probably general in "protected" microhabitats at the end of the season, throughout the northern part of the species range. Characteristics of the emergence are noted in another section, below.

Ova were obtained from four wild females (one *alba*) collected at Erdenheim, Montgomery County, Pennsylvania, 26 November 1967. The larvae were reared at Ithaca on alfalfa, *Medicago sativa* L., at 75°F. in 16 hours light on a 24-hour cycle. The first pupa was formed 20 December and the last 5 January 1968.

Forty-nine pupae were obtained. Sixteen of these were held at 75°F. until a well-defined discal orange flush appeared on the wings, but before the deposition of black border pigment had begun. They were then chilled rapidly to, and held at 36°F. An additional sixteen were allowed to develop full black borders before being chilled to the same temperature. The use of pigment development as a criterion of general condition excluded *alba* females from the first, but not the second group. The remaining seventeen pupae were used as controls. Ten were permitted to develop to eclosion at 75° while seven were chilled 72 hours after pupation, well before the appearance of any wing pigment.

In the two groups of sixteen, four pupae selected at random were removed weekly for each of four weeks and allowed to complete their development at 75°. In both groups all the pupae eclosed, and no cripples were obtained until the third week; even in the fourth only three of the eight butterflies were defective. Most of the pupae which were arrested when less advanced eclosed within 60 hours, regardless of the duration of the arrest, and all within 72 hours. The more advanced pupae all eclosed within 36 hours, mostly within 24; four were observed to eclose within one hour, and one within 35 minutes.

The seven pupae refrigerated at 72 hours were removed after three weeks of developmental arrest. Three were permitted to eclose at 75°, which they did within six days. The remaining four were re-arrested for one week after both orange and black wing pigment had developed. These all eclosed; two were slightly crippled. The ten unarrested pupae produced normal butterflies in seven to ten days.

Three of each group of four butterflies were chilled to 36° within twelve hours after eclosion, unfed and unflown. Eight of the ten 75° butterflies were similarly treated. The remaining butterflies in each group were held unfed and unflown in the dark at 75°. The insects were all examined daily. All controls died within seven days.

Greatly extended survival was noted at 36°; refrigerated butterflies lived from 24 to 49 days. The survival of the butterflies

from previously arrested pupae is summarized in Fig. 1. The unarrested insects lived from 33 to 47 days. Length of adult survival in refrigeration was approximately inversely related to duration of pupal arrest on a day-for-day basis. All of the four-week-arrest insects died within 31 days. Crippling and survival data for these experiments are summarized in Table I.

PIERIS RAPAE AND *P. PROTODICE*

Ten pupae of each of these species, reared in diapause-inhibiting conditions (75°F., 16-hour photoperiod) were arrested at 36° for three weeks at the stage when white, but not black, pigment had been laid down in the wings. The pupae were selected at random from Cornell cultures of the two species, *P. rapae* from third-generation Ithaca, and *P. protodice* from thirteenth-generation Philadelphia stock. Fifteen normal eclosions were obtained within 80 hours. The remaining five butterflies (four *protodice*, one *rapae*) were variably crippled. One of each sex from each batch of normals was held unfed in the dark at 75°; all four died within seven days. The remaining normal insects (four *protodice*, seven *rapae*) were chilled to 36° within twelve hours after eclosion and held at that temperature. *P. protodice* survived 13-26 days and *P. rapae* 15-27.

The Role of Pupal Diapause. — Throughout the Middle Atlantic states, the three species discussed are normally the last non-hibernating butterflies on the wing in autumn. At Philadelphia the last *Pieris* (both spp.) are generally taken from two to four weeks before the last *Colias*, rarely as late as the third week of November. At Ithaca, north of the breeding range of *P. protodice*, *P. rapae* disappears only a few days before *C. eurytheme*; the latest record is 1 November (1967). The mean last capture date for *P. rapae* at Philadelphia in 1959-66 was 12 November, and at Ithaca in 1966-67, 29 October. *Pieris* possesses a facultative pupal diapause mechanism (Barker, Mayer, & Cohen 1963; Shapiro, in preparation) which is lacking in *C. eurytheme*. Diapause is induced by long nights (greater than approximately 11 hours), but inhibited by high temperatures. Under constant laboratory conditions, night lengths from twelve to eighteen hours are equally effective in inducing diapause below inhibition-threshold temperatures. If all of the late larvae in both localities were exposed to diapause-inducing photoperiods, the difference in mean last adult date should reflect the onset of temperatures permitting all pupae to diapause. On the

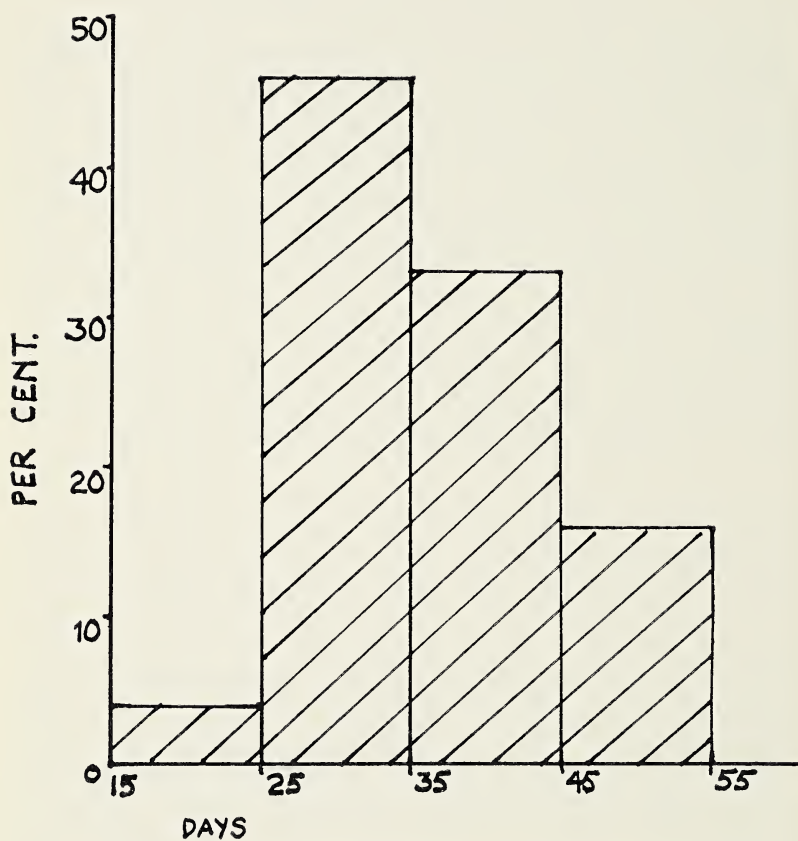


Fig. 1 Survival of 24 *Colias eurytheme* held at 36°F.

Period of Arrest (Days)	Normal	Crippled	Number of Adults Chilled	Mean Survival (Days)
Adults:				
I. Chilled with orange pigment only				
7	4	0	3	45.3
14	4	0	3	40.7
21	3	1	3	35.0
28	3	1	3	29.7
II. Chilled with orange and black pigment				
7	4	0	3	44.3
14	4	0	3	37.7
21	4	0	3	28.8
28	2	2	3	25.7
III. Control				
Unarrested	10	0	8	41.3

Table I.

Crippling and adult survival in *Colias eurytheme* with thermally arrested pupal development.

basis of laboratory growth rates, an estimate of three weeks prior to the mean last date, corresponding to the larval sensitive period of the last emergents, has been made for each locality. Assuming 100% threshold temperatures are the same in both stocks, these two dates should show similar temperature characteristics. The dark period for both is more than twelve and one-half hours, well above the diapause-induction threshold, and the mean temperatures (based on thirty-year United States Weather Bureau data) for Philadelphia, 21 October, and Ithaca, 8 October, differ by only one degree F. One may conclude that an effective 100% diapause is obtained above the threshold night length when the mean temperature reaches the mid-50s. The late-season emergences of *Pieris* are probably analogous to those of *Colias*, but must originate from non-diapause pupae. The phenology of *P. protodice* at Philadelphia is being studied in detail for presentation elsewhere (Shapiro, in preparation).

Temperature Correlations in Colias. — "False broods" of *C. eurytheme* occur regularly at Philadelphia under particular weather conditions in late November, and frequently as late as the first week of December; the latest on record is 16 December (1959). In Tompkins and Cortland Cos., central New York where winter survival of *C. eurytheme* is poor and the population may be replenished annually by immigrants from the south or west, the latest known record is 12 November (1967); the cutoff seems to be generally about 1 November. There is thus a 3- to 4-week difference in the average date of last flight between the two localities. As photoperiodically controlled diapause cannot be invoked, an absolute dependence on temperature would be expected to dictate the end of the season. Mean temperatures and freeze data, based on thirty-year United States Weather Bureau records, were compared for the two localities (Table II). The mean temperature for the last ten days of November at Philadelphia is 40.7°F.; for the last five days of October and the first five of November at Ithaca, 44.8°F. The mean reaches 40° at Ithaca on 12 November. *C. eurytheme* thus disappears in warmer conditions at Ithaca than at Philadelphia, based upon means. The thirty-year mean date of first frost (32°F.) at Ithaca is 4 October and at Philadelphia 25 October. The cutoff for autumnal *Colias* therefore occurs about four weeks after the mean first frost at each locality, the frost dates being three weeks apart. There is no good correlation with the onset of lower sub-freezing temperatures. The deviations below 32° for low temperatures on all sub-freezing nights prior to the 1967

Station	Freeze Threshold Temperature F°	Mean date of first autumn occurrence	Mean number of days between last spring and first fall occurrence
Philadelphia, Pa. (Shawmont)	32	10/25	192
	28	11/09	223
	24	11/23	250
	20	12/06	272
	16	12/17	287
Ithaca, N. Y. (Caldwell Field)	32	10/04	145
	28	10/21	181
	24	11/05	207
	20	11/21	237
	16	11/29	255

Table II.

Freeze data for two stations, 1929-1959. From
 U. S. Dept. of Commerce, Weather Bureau, Climates
 of the States, Pennsylvania and New York, 1960.

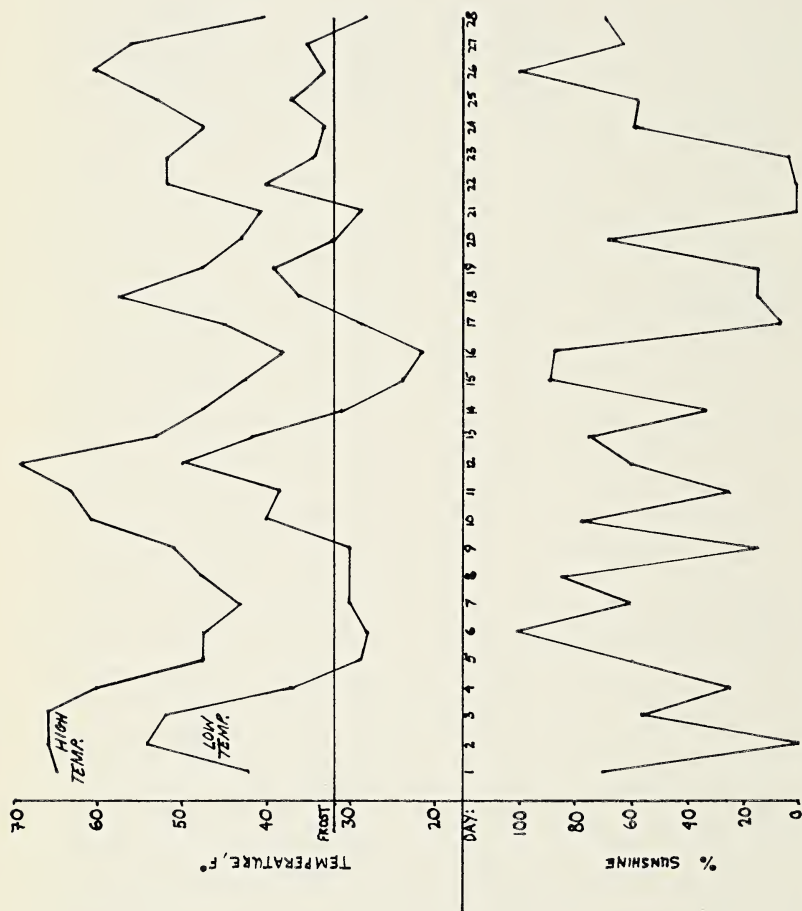


Fig. 2. Weather conditions, November 1-28, 1967. U. S. Weather Bureau, Philadelphia, Pa.

cutoffs summed to 41° at Philadelphia and 44° at Ithaca. If this close agreement is general it would imply that the sequence of temperatures acts in a cumulative way to end the season, perhaps by selective mortality of the most advanced pupae. Degree-hours below freezing might be expected to be a still more sensitive indicator. Close study of day-to-day temperature patterns, including the correlation of data for successive days, should reveal more about the critical factors.

It is easily demonstrable that single frosts, even a severe freeze, do not prevent the subsequent eclosion of autumnal *C. eurytheme*. Fig. 2 shows the weather at Philadelphia during November 1967. Eleven frosts occurred prior to the emergence on the 26th, the most severe reaching 22°F. on the 16th. Fig. 3 shows temperature data for parts of October and November, 1967 with two-hour *Colias* collection totals for each day in the field in upstate New York. At Ithaca there were nine frosts between 12 October and 12 November, with the lowest temperature 23° on 30 October and 7 November.

Case Histories. — The 26 November 1967 emergence was a typical "false brood" at Philadelphia. Butterflies were taken at Erdenheim and Cheltenham, Montgomery County, at localities which regularly produce the earliest vernal and latest autumnal *Colias* I have taken on the southeastern Pennsylvania Piedmont. Both consist of rolling, grassy meadows open to the south and protected by low hills to the northwest. On 25 November, with air temperature 48°, a clear sky, and a 15-mile northwest wind, both were visited but no butterflies were found, either flying or at rest. On 26 November, five male *C. eurytheme* were taken between 1040 and 1130 hours at Cheltenham with air temperature 50-52°F., clear sky, and wind 5 miles from the southwest. At Erdenheim five male and four female (one *alba*) were taken from 1300-1420 hours with temperature 58°, clear sky, and wind 10 miles from the southwest. More butterflies probably appeared at Cheltenham later in the day. One Erdenheim male was not fresh, but the other 13 butterflies were very fresh, and three were soft-winged.

In central New York, *C. eurytheme* was present continuously through 24 October. Heavy rain occurred on the 26th, followed by brief clearing the morning of the 27th and passage of a cold front in the afternoon. On the 27th two old *eurytheme* males were taken at rest in overcast (temperature 45°F.) at the Ithaca City Dump. A female *C. philodice* Latreille was also taken in flight during a sunny interval. Cloudy, windy weather then set

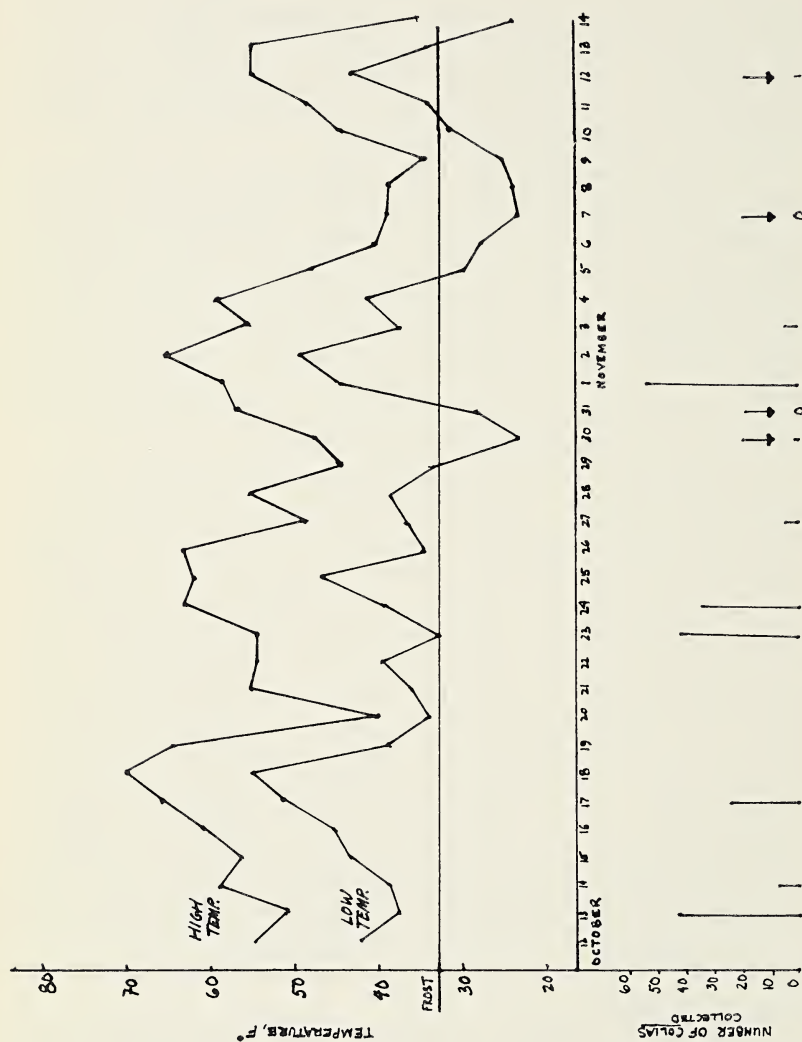


Fig. 3. Temperatures and *Colias* collections, October-November 1967. Ithaca, N.Y.

in. After a heavy freeze the morning of 30 October, a male *C. philodice* was taken on the Cornell University campus at 1400 hours with clear skies, a light southwesterly wind, and air temperature 46°F. A warm front passed on the 31st with heavy overcast. A "warm pocket" at Gracie, Cortland Co., was visited but no butterflies were found, despite an air temperature of 56°F. On 1 November it was clear, and *C. eurytheme* was found abundant at Gracie and at the City Dump. The air temperature in early afternoon was 58°. At Gracie 27 male and five female *eurytheme*, five male *philodice*, and five undetermined *alba* females were collected in 90 minutes; all but six were clearly fresh, and fourteen were newly eclosed and soft-winged. One male was taken sitting on its pupal case. The six older insects were obviously flown and might have emerged on the 30th or during the preceding warm period, before the 26th. There were only two freezes between the 26th and the 1st, but that of the 30th was quite severe. At the Dump eight male and two female *eurytheme*, including a pair in copula, and two male *philodice* were taken. All were very fresh.

The four *C. eurytheme* taken at the Dump on 3 November, and the one female taken there 12 November, were likewise all very fresh in appearance.

Reproduction and Selective Aspects. — Although reproduction by "false broods" would appear doomed, females of all three species usually contain a spermatophore when taken. Pairs in copula are common, and a great deal of sexual behavior, including male "darting-searching" of low vegetation and male-male chases, may be observed. This cannot be attributed to lack of flowers, as dandelions are usually present and visited repeatedly. As a behavioral adaptation to low temperatures, rapid initiation of sexual activity would be highly advantageous in insuring successful reproduction in the spring. A disproportion in sex ratio generally occurs in autumnal *Colias* emergences, with males two to four times as numerous as females. The same phenomenon occurs in the early stages of the spring emergence, but the sex ratio corrects itself in time. It is thus probably an artifact of the slightly slower development of the female. In both cases the result is generally the mating of unflown, newly-eclosed females, which may conserve energy for the latter. No differential sexual effect was noted in the arrestation experiments, except for a slight lag in the time of pigment deposition in the female pupae prior to arrest.

Mansingh and Smallman (1968) discuss precocious development in the Saturniid *Antheraea polyphemus* Cramer in North Dakota. This species is normally univoltine in the locality studied, and the timing of the single generation depends on weather conditions in the spring. An unusually early adult emergence from the overwintering pupae would permit some of their offspring to complete their development under non-diapause-inducing photoperiods and to emerge the same season (i.e. too late to reproduce), or to be frost-killed as pupae. These authors suggest that "early pupation can, under certain environmental conditions, become a serious mortality factor" in *A. polyphemus* (*loc. cit.*, p. 138). This is essentially analogous to the condition prevailing in the autumn broods of Pierids. Wastage of gametes at the end of the season should result in selective pressure for development of a timing mechanism effectively independent of temperature (i.e., photoperiodically induced diapause), except on a season-indicating threshold basis in multivoltine species. (*A. polyphemus* is partially or completely bivoltine southward, with a non-diapausing summer and a diapausing winter generation.) The duration of the developmental arrest should be adjusted to the onset of favorable conditions in the spring at each locality. This appears to be the case in *Pieris*. Both *P. rapae* and *P. protodice* are genetically polymorphic for duration of diapause under constant temperature conditions, and strains differing in induction ranges, temperature thresholds, and length of diapause can be selected (Shapiro, in preparation). Differences in microclimate undoubtedly maintain these polymorphisms in the population, resulting in a wide range of potential response to the year-to-year vagaries of weather.

In *Colias eurytheme* some sort of adjustment to winter survival appears to have taken place shortly after its invasion of the Northeast (Clark 1932). Although the species overwinters successfully every year at Philadelphia today, its tendency to produce a "false brood" is greater than that of any other Pierid species found there, and it still lacks a true diapause inducible in the larval stage. It begins to fly four to six weeks later than the *Pieris* species in spring, however, and the possibility exists that prolonged chilling may induce diapause or a diapause-like condition after pupation. Some half-grown larvae are apparently capable of overwintering at Philadelphia, but attempts to carry them through at Ithaca, outdoors or in a refrigerator, have failed.

ACKNOWLEDGEMENTS

The author wishes to thank the Sisters of Saint Joseph for permitting the use of the grounds of Mount Saint Joseph Academy, Erdenheim, Pa. for field studies of *Colias eurytheme* from 1959 through 1967. The alfalfa plants used in the rearing were provided by Edward L. Rittershausen. Messrs. Rittershausen, James D. Biggs, and J. Warren Webb assisted in the field observations in New York.

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POLYCTOR POLYCTOR (PRITTWITZ) IN MEXICO (HESPERIIDAE)

H. A. FREEMAN¹

1605 Lewis Drive, Garland, Texas

WHEN GODMAN & SALVIN RECORDED *P. polyctor* (Prittwitz) from Mexico to South Brazil they were unaware that they were dealing with two separate species in their available material. They gave as the habitat of *polyctor*.-Mexico, Acapulco (H. H. Smith), Jalisco (Schumann), Atoyac (H. H. Smith, Schumann), Cordoba (Rumeli); Guatemala, Volcan de Santa Maria (W. B. Richardson); Nicaragua, Chontales (Belt); Panama (Champion).-South America, from Colombia to South Brazil. Apparently Hoffman followed, in part, the data furnished in the Biologia Centrali-Americana when he prepared his Hesperioidea of Mexico as he listed *polyctor* as occurring in that country. — "Tierras caliente y templado-calida de Campeche, Tabasco y Veracruz. Por el lado del Pacifico de Guerrero a Colima." (Hot and warm temperate lands of Campeche, Tabasco and Veracruz. On the Pacific side from Guerrero to Colima).

Evans recognized the presence of two separate organisms in the material present in the British Museum and described *cleta* as a new subspecies of *polyctor* based on specimens from Mexico, Guatemala and Costa Rica, and he used a male from Acapulco, Guerrero as the holotype. His basis for recognizing a difference between *cleta* and *polyctor* was due to two factors: (1) in *cleta* the cell spot on the primaries is white and hyaline, whereas in *polyctor* the cell spot is opaque; and (2) differences in the genitalia. His recording of both *cleta* and *polyctor* from Costa Rica and the differences in the genitalia indicated to me that he was confused in his usage of the term subspecies as applied to *cleta*. After carefully examining specimens in my collection I found two males of *polyctor* that had been collected at Acahuizotla, Guerrero during the same month as specimens of *cleta* from the same locality. Superficially the two species are very similar, however, there are other differences besides the two things mentioned by Evans that help in separating *cleta* and *polyctor*: (1) the white band on the primaries does not ex-

¹I would like to express my thanks to the National Science Foundation for Research Grant GB-4122 which is making this study of the Hesperiidae of Mexico possible.

tend to the costa in *polyctor* and it does in *cleta*; (2) the width of the white band in the cell of the primaries is twice as wide in *cleta* as it is in *polyctor*; and (3) the black area beneath the spot in space 2 is directed straight toward the inner margin in *cleta*, while in *polyctor* it is angled basad in space 1b.

POLYCTOR POLYCTOR (Prittwitz), 1868

Type locality. — Corcovado, Rio.

Distribution. — Mexico; Costa Rica; Nicaragua; Panama; Colombia; Venezuela; French Guiana; Ecuador (R. Napo); Peru (Rentema Falls, Chanchamayo, Perene, Amazonas); Bolivia (Buenavista, Santa Cruz, San Jose, Mapiri, Tanampaya, Cochabamba, Yungas, La Paz); Upper Amazon (Iquitos to Santarem); Goyas; Minas Geraes; Pernambuco; Matto Grosso; Brazil; Pasaquay; and Argentine.

Mexican distribution. — Acuahizotla, Guerrero, July and September, 1960. Specimens obtained from Dr. Tarsicio Escalante, Mexico, D. F.

Remarks. — This is the first authentic record for this species from Mexico. Apparently all previous records of *polyctor* for this country apply to *cleta*.

Type locality. — Acapulco, Guerrero, Mexico (September, H. H. Smith).

Distribution. — Mexico; Guatemala; and Costa Rica.

Mexican distribution. — Acapulco, Acahuizotla (July and September, 1960), Guerrero; Jalisco (Schumann); Colima (Hoffman); Tamazunchale (June 19, 1964, H. A. Freeman), San Luis Potosi; Atoyac (H. H. Smith, Schumann), Cordoba (Rumeli), Catemaco (A. Ramirez), Veracruz; Campeche (Hoffman); and Tabasco (Hoffman).

Remarks. — There is no doubt as to the specific validity of *cleta* since both species occur together at Acahuizotla and their genitalia differ considerably in the shape of the claspers, and also the general shape of the uncus as can readily be seen from the ventral side. This is a remarkable example of a sibling species flying in company with its nearest relative.

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ECOLOGICAL COLOR VARIATION IN SOME ARGYNNIS OF THE WESTERN UNITED STATES

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THE COLOR PLATE ON THE BACK HEREOF represents a color rendition of figure 4 in a paper previously published (Hovanitz, 1941). That figure shows a black-and-white reproduction from the same color transparency that was used in this color reproduction. The title of the figure 4 mentioned is "*Geographical variation in five species of Argynnis in California. (1) Argynnis callippe* (Coast Range cline), (2) *Argynnis callippe* (Sierra Nevada cline), (3) *A. monticola*, (4) *A. adiate*, (5) *A. zerene*. This figure should be used in conjunction with the map (fig. 5) as the numbers and letters thereon refer to the specimens shown in this figure." On the color plate the numbers and letters are not shown as they are in the black and white rendition but can be construed as follows: the columns are numbered from left to right from 1 through 6. whereas each specimen is lettered from top to bottom from a through e.

Approval has been obtained from the publishers of the JOURNAL: ECOLOGY in which this article was first published for reprinting in this JOURNAL and this will be accomplished in one of the next few issues.

REFERENCE

HOVANITZ, WILLIAM. 1941. Parallel ecogenotypical color variation in butterflies. *Ecology* 22: 259-284.



NATURAL HABITATS

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA is starting a continuous series of illustrations of natural habitats. This series will include general as well as specific illustrations of habitats, ecological niches, of food plants of LEPIDOPTERA.

The purpose of this series is to show from an ecological standpoint the type of habitat or niche in which a particular species or race is to be found; in addition, the purpose is to record these for historical purposes. Many habitats are being destroyed yearly by the encroaching "civilization". For example, most of the habitat for Glauropschye xerxes and Plebejus icariodes pheres-missionensis has been destroyed in the area of San Francisco and these are now most likely extinct races or species. The largest part of the popular collecting locality at the mouth of the San Gabriel River canyon near Azusa, California has just this year been almost completely obliterated. The illustrations which follow show the small remaining portion of that once extensive area.

LEPIDOPTERISTS, whether members of the FOUNDATION or not, are urged to submit photographs of habitats for inclusion in this series. Each should be accompanied by a short description of the locale, the name of the species or race concerned and if possible an illustration of and the name of the food plant. Each submission will be acknowledged.

WILLIAM HOVANITZ

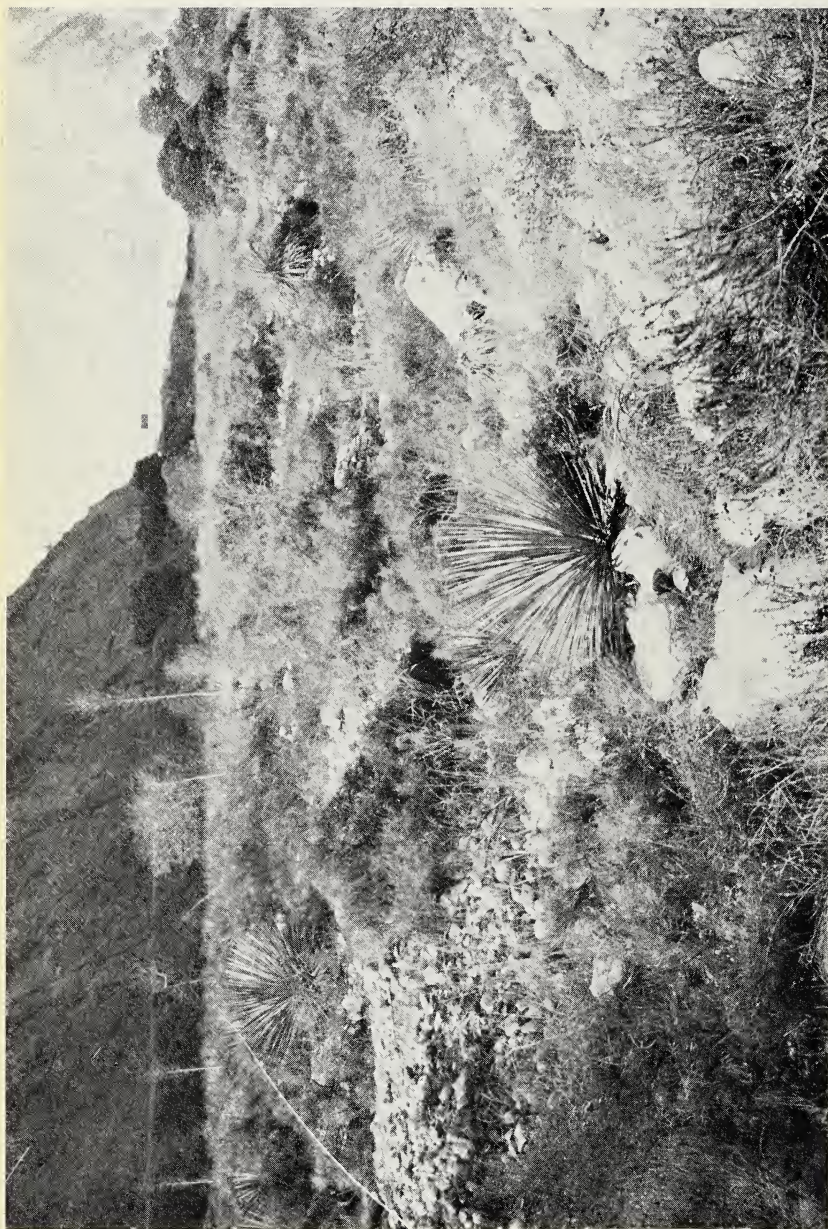


Fig. 1. Habitat at the mouth of the San Gabriel River canyon just north of Azuza, California looking southwest. The area in the immediate foreground is the location where the next two photos were taken. Under the bushes shown grow the food-plant (Dudleya lanceolata) also known as Rock Lettuce or Desert Savior, a member of the

J. Res. Lepid. 1(4): 237-244, 1963). In the distance may be seen a portion of the rock pile that is nearly all that is left of the formerly much wider range of the species at this location.



Fig. 2. Dudleya lanceolata, shown by arrow, as exposed by pushing the brush away.



Fig. 1. Habitat at the mouth of the San Gabriel River canyon just north of Azusa, California looking southwest. The area in the immediate foreground is the location where the next two photos were taken. Under the bushes shown grow the food-plant (*Dudleya lanceolata*) also known as Rock Lettuce or Desert Savior, a member of the *Crotonaceae*. This is the food plant in this area for *Philotes sonorensis* (see Mattoni and Seiger: Techniques in the study of population structure in *Philotes sonorensis*, J. Res. Lepid. 1(4): 237- 244, 1963). In the distance may be seen a portion of the rock pile that is nearly all that is left of the formerly much wider range of the species at this location.



Fig. 2. Dudleya lanceolata, shown by arrow, as exposed by pushing the brush away.



Fig. 3. *Dudleya lanceolata*, as shown by arrows, exposed by pulling away the brush from over the plants.

ESTIMATING THE DENSITY OF AN ANIMAL POPULATION

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INTRODUCTION

Obtaining valid data on the number of animals in a population, estimating the density from these data, and determining the confidence limits of the estimates, together are basic to investigations in ecology. Although "good" estimates of population density are highly important (Odum, 1959:150), they are usually difficult to make, particularly among animals as mobile and wary as winged insects and most vertebrates. The problems arising during population estimation have at some time hampered most ecologists, and, hence, efforts to overcome the difficulties have led to the proliferation of a rather vast literature, which is more or less widely scattered. Therefore, it is proposed to review some important developments in the still rapidly-expanding field of density estimation and to describe a few major procedures that are recommended to insect and vertebrate ecologists. No attempt is made to be "thorough," because that would require a large book, in fact, an encyclopedia. One or more representative types of each of the major kinds of procedures based on sampling of the animals are, however, discussed.

In spite of the fact that obtaining valid data is absolutely prerequisite to the use of density models, methods for obtaining the valid data are not taken up here. The latter would, for one thing, extend the scope of this review to excessive length; and, moreover, each field study is unique to a great extent, requiring usually some unique activities to get these data. Although it is apparent to all that no amount of tedious analysis gives useful results when the data are biased and the bias cannot be removed, yet most of us are too prone to assume that satisfactory data has been obtained, especially when an equation is used to manipulate the figures. Analysis of several kinds of data, used in several different mathematical models, should of course lead to results that approximately agree. If they do not, further

information should be collected and analyzed by the same and other methods to obtain convincing evidence of the most probable density. Good data are the heart of density estimates!

Excellent general reviews of the methods for obtaining the figures and analyzing them, with special reference to vertebrates, have been published by Ricker (1958), Davis (1963), Scattergood (1954), and others. Of special interest to entomologists is the fine book by Southwood (1966); the first 228 pages are on estimating population density, both in an absolute and a relative sense, and considerable is given on how to obtain the data. This book and one by Ricker (1958) are the two best publications available today on the subject of estimating population density of animals, but due to its younger age and emphasis on insects, the book by Southwood is the most valuable publication on the subject for entomologists. Andrewartha (1961), Menhinich (1963), and others have published shorter reviews (but good ones), with emphasis on the insects. Detailed reviews dealing with some restricted groups of methods have been provided by Chapman (1955), Hanson (1963), and others. In his review, Davis (1963:91) pointed out that the supposedly large number of sampling methods for determining the number of animals actually rest on one of three basic classes of enumeration, either (a) true censuses of the whole population, (b) sampling of the animals themselves (rather than of their sign), or (c) indices to the population, involving either the animals or their sign. (Indices are of course the ratio of the number of animals seen to the number of some unrelated kind of object, such as the number of butterflies seen per mile of roadside; or the number of tracks per linear unit of pond margin, or the number of an insect's eggs per leaf of certain plants, etc.).

Concerning the three general classes of enumeration, true censuses are in actual practice rarely attempted because of their excessive cost and because some of the animals may escape counting. Ideally, a true census is most practical when the animals are large and live in habitat where they are easily seen; on the treeless plains of North America and Africa, big game are thus sometimes censused from aircraft, but even then the areas covered are frequently not large. For the average ecologist, a true census of a whole population, or even a small segment of it, is usually out of the question.

On the other hand, indices are often highly feasible and yield valuable information, but that information hardly ever can be converted into estimates of population density. In many prac-

tical investigations, it is enough to know that a population has increased or decreased by a certain amount, relative to some long-time set of indices, and thus a mere trend in density, rather than the absolute population density itself, is sufficient. Very often, however, the investigator needs to know more, and thus he is forced to turn to sampling, the random counting of some fraction of the population, and the subsequently extrapolating to the whole population. All further material in this paper will deal with sampling of the animals themselves.

The sampling techniques turn out to be of four general types: (a) a count of all animals on sample plots of known size, (b) marking, release, and re-observing of animals, (c) changes in catch-per-effort or changes in sex or age or other ratios caused by removal of a known number of animals, or (d) analysis of statistical properties of the data's distribution.

Moreover, regardless of the basic class of sampling employed, it nearly always requires a total count of some population component. Even in the mark-and-recapture method, while one component is being made recognizable by marking it, the observer ends up, in effect, making a total count of the marked group and must use this total in later computations. Regardless of how the total count of a population component is obtained, much effort will usually be required, and in many cases the data may still contain biases. In certain situations the work may be restricted by well-known difficulties, such as trap-shyness of the animals, loss of marks, natural segregation of animals by sex or age, uncertainty that all animals on sample plots have actually been seen, ingress and egress from study areas, and many other problems. Now, some of the principal methods based on sampling of the animals (not of their sign) will be described.

TOTAL COUNTS ON SAMPLE PLOTS

In this well-known method of estimating population density, some fraction of a study area is sampled intensively and the results are extrapolated to the total area. The major assumptions behind the method are: (a) The animals are sampled at random, and (b) all of the animals existing on each plot are counted, but are counted only once. The method presents relatively little complexity from the standpoint of analyzing the data, but obtaining reliable data is often quite difficult, especially for insects that are more or less hidden or inaccessible, either in plants,

in the soil, inside of other animals that are being parasitized, etc. Southwood (1966:99-228) has devoted the majority of his material on estimation of density to the matter of total counts on sample spaces and has given a fine treatment of methods for collecting the insects or otherwise getting the required data.

As usual, the investigator will want to find the mean number of animals seen on the sample plots, \bar{x} , and the variance of the sample mean, s^2 . From these, he should calculate the confidence limits of his estimated total population, \hat{K} . Thus, if he estimates that 50 animals (as in an insect population) are present per sample plot but that the 95% confidence limits are ± 10 , then the true value should be between 40 and 60 of the insects per plot. Moreover, if the investigator has sampled only 1% of the total study area, then the estimated abundance on the whole study area, \hat{K} , ranges from 100 times 40 to 100 times 60; that is, \hat{K} would lie between 4,000 and 6,000. Let us now return to the major assumptions underlying the procedure.

To sample the animals at random, the observer samples the area at random, and assumes axiomatically (not requiring further proof), that this leads to a random sample of the animals. Ecologists have frequently pointed out (see Cole, 1946, for example) that animals are seldom distributed at random. Will this negate attempts to obtain a random sampling? When the animals are highly clumped, most of the sample plots will be "blanks," i.e., have no animals on them, while a few of the plots will have a great many animals. Nevertheless, one can still take a random sample of the animals by making a random sample of the study area — because plots with animals and plots with blanks should be encountered with a frequency that corresponds to their frequency over the entire geographical extent of the study area. At least that is the statistical expectation when the work is done properly. This is most important. Some ecologists have claimed that statistical theory is automatically invalid when animals are not spatially distributed at random, but such ideas are, to put it tritely, "highly erroneous." Clumping of animals does not necessarily invalidate statistical theory, but the presence of many plots with no animals and a few plots with many animals does lead to a high variance that results, finally, in wide confidence limits for the estimate of mean density of the whole population.

The data may form (a) a (positive) binomial distribution if each animal has the same probability of being observed, if this probability is not too small, and if the counts of the animals are

independent, i.e., if the observations have no clumping or "contagiousness." The data may form (b) a Poisson distribution if the same conditions hold except that the probability of observation is very small, actually a more common possibility in extensive surveys rapidly conducted over larger areas. (Nevertheless, in total counts on sample plots, the observer is determined to find all or nearly all of the animals regardless of how small this probability of observation may be.) The data may form (c) a negative binomial or other distribution if the animals are contagiously distributed, which is a very common phenomena in nature, as indicated above. It is well known that the ratio of variance to the mean, s^2 / \bar{x} , indicates the degree of contagiousness of the data. In the (positive) binomial distribution, the variance is less than the mean, in the Poisson the two are equal, and in the negative binomial the variance is bigger than the mean.

Grieg-Smith (1964), Kershaw (1964), and others have discussed the use of the ratio s^2 / \bar{x} for detecting patterns of non-randomness among plants. Kershaw (pp. 104-108) gave data analyzed by Grieg-Smith and diagrams and a nice discussion showing how the size of the quadrat affects the distribution of the data. As quadrat size is increased, the data for organisms which are actually clumped will show, successively, a random, contagious, and regular distribution. The most marked contagion results when the quadrat size is about the same as the average area of each clump of organisms.

Although the investigator who is trying to estimate the population density of animals from total counts on sample plots requires to keep the variance of the counts fairly low, he is confronted by a dilemma. If plot size is increased; it reduces the variance due to clumping; but at the same time the increase in the size of individual plots often leads to a reduction in the number of plots which can be searched, a factor that increases the variance again.

Hanson and Chapman (in press) proposed that, where clumping was a marked problem, the number of "clumps," i.e. groups, of animals be counted as well as the number of animals in each group because the distribution of the groups should tend to be at random. Laboratory populations of mealworms (*Tenebrio molitor*) were studied from this standpoint, and experimental estimates of their density were improved by counting clumps. Regardless of the procedure that the ecologist hopes to follow, he should of course consult a statistician before planning his

field surveys and at intervals thereafter to modify the surveys as required by problems encountered.

Therefore, the intensity of the sampling that one should do depends on the degree that the animals clump, and the degree of precision required. According to the writer's experience, it is difficult to estimate the density of a population within 20 per cent of its true value, by any practical method, and even this degree of precision usually requires intensive sampling. In fact, Davis (1963:117) said that investigators "will have to spend fantastically greater time and money on estimates than has been done in the past, if they wish to detect changes of much less than 25-50% of the population."

The size of sample that is required to give any desired size of confidence interval is covered by most textbooks of statistics, for example, Snedecor (1946:457). The standard equation for the statistic t is solved for the sample sizes; it may be remembered that the definition of t is

$$t = \frac{(\bar{x} - \mu)}{s_{\bar{x}}}$$

where as usual \bar{x} is the mean of the sample; μ (μ) is the true, but unknown mean of the whole population; and $s_{\bar{x}}$ is the standard error of the mean, that is to say, s / \sqrt{n} . The symbol s refers, of course, to the standard deviation, which is the square root of the variance estimate, s^2 . After the expression equivalent to the standard error, s / \sqrt{n} , is substituted into the definition for t , the equation is then solved for n , specifically the sample size required in order to achieve any desired level of confidence for any selected permissible error, viz.,

$$n = t^2 s^2 / (\bar{x} - \mu)^2.$$

The investigator must decide on the amount of error that he can tolerate and substitute this in place of $\bar{x} - \mu$, and he must decide on the degree of confidence he wishes and look up the corresponding value of t in the tables given in most textbooks of statistics. It may be useful to remember that when the sample equals 60, t equals exactly 2.000, and that as n increases beyond 60, t changes so little that in empirical work the value of t can be safely called just 2. To illustrate concerning the allowable amount of error, one might expect, for example, that \bar{x} would be about 20; but that an error of 15%, or 3 (i.e., 15% of 20), would be tolerated. Thus, 3 would be inserted in the denominator of the equation for sample size, and it would be squared to become 9.

To use this equation properly, the investigator must have some *prior* knowledge of the variance to be expected. If this prior knowledge were already at hand, the normal procedure would be to then (a) while in the office, estimate the size of sample that is required for the definitive study, and (b) go in the field and collect this sample. Where is one going to get a prior knowledge of the expected variance? It must either come from previous attempts to sample this same population, by essentially the same methods that are now used, or one must make a special pilot study to get the estimate of s^2 . That is, if necessary, the worker takes a smallish preliminary sample of the population in the regular way and calculates its variance; the resulting value is then inserted in the equation just given to estimate how big the subsequent main sample must be. Note that one cannot take a sample of the population and then, *a posteriori*, say that the sample was big enough. All one can do is to say that future samples — if taken the same way — will have to be equal to, or greater than, some calculated number in order to give the required precision with the required level of confidence.

What should the investigator do to get random samples? First, he usually should *on paper* divide the study area into numerous equal-sized plots. If fairly large areas are involved, the most convenient way to do this is to take an aerial photograph of the study area enlarged to perhaps 10-15 centimeters of photograph per linear kilometer on the ground and to lay out on the photograph a grid of lines that is so constructed as to give the desired number of plots, and then one should give each plot a permanent identifying file number. Finally, the plots to be studied should be selected by drawing their file number from a table of random numbers, such as the table given by Fisher and Yates (1957:126-31) and many authors in textbooks of statistics. This process will tend to rule out human choice of plots to be sampled, and it is usually the most practical way to obtain a random sample on land. Therefore, in terrestrial ecosystems the first of the major assumptions mentioned above can be met, although sometimes, just by chance, and with a probability he can calculate, the investigator will get a "bad sample," in the sense that it will not be very representative of the whole study area. Random sampling in aquatic ecosystems is much more difficult since the space sampled is a volume and boundaries are difficult to establish, a matter which will be commented on further below.

The second major assumption included the idea that all of the animals present on the study plots were counted, but this will almost never be possible unless one is working with large plants, or elephants, or other very large and visible animals. Little need be said on this point, for the most convincing arguments are furnished by each reader's own field work. No matter how carefully the plots are searched, some of the animals are likely to be missed unless the plots are very tiny and searched diligently. There seems to be no practical way to estimate the amount of error caused by not finding all of the animals except to do the "total" counts repeatedly and calculate "efficiency" by the method of Seierstad *et al.* (1967), or to compare results to those obtained from a completely different model.

The highest number seen would, of course, usually be considered the best number, but it could be inflated by chance influx of animals on to the plots from peripheral areas.

Included in the second assumption was the idea that very few or none of the animals were counted more than once, but this may not be true in practice. The assumption is most likely to be met in animals of low mobility, especially when the animals make no particular effort to avoid the observer, as in insect larvae, snails, etc. On the other hand, when dealing with highly mobile animals, such as most adult butterflies and many other arthropods and vertebrates and some members of other classes — some counted animals may move rapidly away from the observer and end up on another plot where they will probably be counted again. However, it is much more likely that, if an animal is unusually mobile, it will flee from the plot before the observer counts him; and is is not likely to be counted later. Thus, in work on highly elusive animals, the method of "total" counts on sample plots frequently gives under-estimates.

In summary, the three major assumptions are difficult to meet, and, hence, "total counts" on sample plots often yield only poor estimates of population desnsity. Although randomness of samples can be attained, the plot size and the sample-size must be increased as clumping increases. Some animals are usually overlooked and not counted, even when searching for them is thorough and careful, but this error may be partially counteracted by the fact that other animals were counted twice or more. Where animals are comparatively wild and mobile, as among many of the insects and vertebrates, the estimates will often be biased downward. Nevertheless, the procedure is

widely used and in many cases is the most practical method of sampling.

In the past, investigators have had no good way to establish whether or not important sampling error occurred when making "total" counts on sample plots, except to estimate population density with several different models and sources of data to see if results approximately agreed. Very recently, however, Seierstad, Seierstad, and Mysterud (1967) gave two procedures for estimating the efficiency of surveys designed to yield total counts. The first of their two methods requires that repeated counts be made on the sample areas, and evidently during each of these the observers attempt to find all of the animals. Due to random events, the total number of animals seen during each complete survey tends to vary somewhat. Seierstad *et al.* assumed that X_i individuals are seen in each total survey (for all sample plots combined) and, furthermore, that the X_i 's are independently and binomially distributed. They found that the estimated probability of seeing one specific animal, \hat{p} , was given by

$$\hat{p} = 1 - \frac{s^2}{\bar{x}}$$

After \hat{p} was found, one could of course estimate the total abundance on the sample area from the ratio \bar{x} / \hat{p} . A formula for the estimated variance of \hat{p} was included.

Further details of this procedure of Seierstad *et al.* (1967) will not be mentioned because it seems to result in the same estimator that was derived independently by Hanson and Chapman (in press). The latter workers, however, designed their own method as a primary estimator of population density in its own right when rapid, incomplete counts were to be made, not to determine survey efficiency of total counts. Near the end of the present report the procedure of Hanson and Chapman will be described briefly. The method of Seierstad *et al.* mentioned above and their other one are valuable attempts to give checks on the efficiency of so-called total counts. However, their report did not mention experimental tests of the method and it did not comment on the fact that data from individual animals are seldom distributed binomially.

Before leaving the matter of total counts on sample plots, a peculiarity should be noted; the method normally presumes to apply to areas, whereas animals such as insects, birds, and fishes usually move about in volumes. For example, if the in-

investigator were studying the question of how many insects of some tree-inhabiting species lived on each "unit area" of a forested tract, he would probably take a volumetric measurement by estimating the number in insects per tree (or per part of a tree) and multiply by the number of trees per unit area. This presents no difficulty in theory except that such estimates do not fit the usual definitions of density and cannot be readily compared to those that do pertain essentially to two-dimensional space. Partly because of this difficulty and also because it is hard to delimit the boundaries of sample plots in aquatic habitats, fishery workers and some other kinds of specialists have emphasized the marking procedures for estimating population abundance or density or both, the subject of the next section.

ESTIMATING POPULATION DENSITY BY MARKING

Introduction

Probably more has been written about estimating density in this way than by all others combined. Chapman (1948) and Schaefer (1951) found that the procedure dates back at least to La Place in 1783, who used the method, in effect, to estimate the human population of France; but Petersen (1896), working in Denmark on fish, is often said to be the first to estimate the abundance of nonhumans in this way. Bailey (1952) and LeCren (1965) believe, however, that Petersen did not use marking to estimate density although he used it for other purposes. Rather, according to LeCren, Dahl (1917) in his book on trout was the first to publish the use of the method on animals. His procedure was explained again in a condensed English translation (Dahl, 1919). Thus, it is not justified to call such marking methods the "Lincoln Index," since Lincoln (1930) did not publish on the matter until later. In the period since 1930, many writings dealing with elaborations of the basic model have appeared, and equations for confidence limits have been derived. The best overall summary and interpretation of the extensive literature so far is that of Ricker (1958). There is much of value on this and many other aspects of population dynamics in the important book by Beverton and Holt (1957). Southwood (1966:57-98) gave a highly useful discussion of the method of estimation based on marking, and he reviewed and cited much literature on the subject.

As is becoming widely known, the underlying idea of the marking methods is that some animals of a population will be

caught, marked alive, and released back into the general population. After the marked animals distribute themselves around to become mixed up with unmarked ones, a new sample is captured, and the fraction of this second sample containing marked animals is determined. Knowing the total number marked, and the effect this total of marked animals had on a later sample — by causing a certain fraction of the sample to bear marks — the investigator can quickly perform the simple arithmetic required to estimate the abundance of the whole group studied.

Although it is most usual to mark the animals artificially, the theory of the method is equally applicable to animals which bear natural marks. Likewise, although it is most usual to recapture the animals, re-observation of free-ranging, noncaptive animals is also adequate if the artificial or natural marks can be distinguished during the second period of sampling.

As usual, valid data must be obtained, and often that is very difficult. Ricker (1958:86) listed several conditions that must be met in order to justify the use of the most basic model on fish populations. These conditions would apply to other populations as well and they are:

1. Marking does not increase natural mortality.
2. Marked animals are neither more nor less vulnerable to the recapturing operations than are unmarked ones.
3. The marks do not come off the animal or otherwise become invisible (as in the case of dyes which fade out), and they are recognized and reported.
4. Either the marked animals mix up randomly with the unmarked ones, or, at least, the second sampling and recapturing is at random with respect to the locations of the animals as a whole.
5. There is little, if any, recruitment to the population.

To Ricker's list here, one can add a further well-known restriction, that

6. Marked animals do not leave the area of study and do not, in effect, become replaced by unmarked ones which move in.

It should be noted that the fifth and sixth requirements above lead to one basic condition, that the fraction of the population bearing marks does not change. Procedures to follow when this fraction does change become somewhat "involved" but are well covered by Ricker (1958:111-144) and others. Steps that might be taken to offset lack of fulfillment of the other conditions were also discussed at length by Ricker (1958:86-100). Obviously

the shorter the time between the two samplings the less the possible effect of recruitment or movement of marked animals out of the area.

Two Samples Taken

The original Dahl (or Petersen) Estimator required two samples only; after the samples were taken a proportion was established that said basically the following:

$$\frac{\text{Number of Animals in Whole Population}}{\text{Number of Animals in First Sample, All of Which Are Marked.}} = \frac{\text{Number of Animals in Second Sample}}{\text{Number of Animals in Second Sample That Had Marks.}}$$

The equation can be solved for the number of animals in the whole population, but the solution is slightly biased and \hat{K} , the estimated total population or segment being studied, diverges more and more from K , the actual total population or total of a segment, as the sample becomes smaller. Several workers have, therefore, proposed helpful refinements of the basic equation indicated above in words, of which one by Bailey (1951) is

$$\hat{K} = \frac{X_1 (X_2 + 1)}{X_{1,2} + 1}$$

X_1 is the total number of animals in the first sample and all are marked after their capture, X_2 is the total number in the second sample, and $X_{1,2}$ is the number among the second sample that bear marks. The latter symbol carries the subscripts "1,2" to indicate also that these animals bearing marks have to be ones which were caught twice, that is, in sample 1 and sample 2.

The addition of 1 to X_2 in the numerator and of 1 to $X_{1,2}$ in the denominator, Bailey's refinement, has important consequences in small samples, where usually $X_{1,2}$ is especially small, but in large samples the corrected equation of Bailey gives results nearly the same as in Dahl's original expression.

The investigator should, as usual, calculate the variance of \hat{K} so that he can find the confidence limits of his estimate of abundance. Although better methods of calculating the variance have been found (see the review of Ricker, 1958:84-85), it is usually adequate to approximate the confidence limits by reading directly from tables of limits for the binomial distribution, especially if an appreciable fraction of the population is marked, say 8-10% or more.

When looking at tables or charts giving the binomial confidence limits, what is the random event which is initially being studied? The random event is the question of whether or not any given captured animal in the second sample bears a mark; each animal is marked or is not, and finally after looking at all the animals in the second sample, the investigator can establish an estimate of the probability, \hat{p} , that any given animal in the whole population is marked. From an appropriate table, such as Snedecor's (1956:4-5), one looks up the confidence limits for the probability that was calculated from the sample. Suppose that a second sample of some particular size had 0.2 marked animals and that the binomial table (for the particular sample size and selected level of confidence) showed its confidence limits to be ± 0.05 . Therefore, \hat{p} was expected to vary from 0.15 to 0.25. As a result, $X_{1,2}$ in the Dahl Estimator would vary up or down accordingly. As one might suspect, the investigator solves the equation for \hat{K} twice, using first the lower limit for \hat{p} and then the upper limit. Some people prefer to use the Clopper-Pearson charts where the confidence belts are shown in graphic form for various sample sizes. Adams (1951) reproduced several of the charts for the binomial confidence limits, as well as several for the Poisson limits, and gave a good discussion of their use. The Clopper-Pearson charts of the binomial limits are also shown in some textbooks of statistics, such as the one by Steel and Torrie (1960:458-459).

To take another example, suppose one found from two samples, involving marking and later recapturing, that X_1 equalled 100 and X_2 also equalled 100, but $X_{1,2}$ equalled 20. Therefore, \hat{p} (the estimated probability that any given animal in the whole population would bear a mark) in turn equalled 20/100. Thus, for some selected level of confidence, say the 95% level, $X_{1,2}$ would be within these limits (Snedecor, 1956:4-5):

$$13 < X_{1,2} < 29$$

Finally, although the best estimate of K would be

$$\hat{K} = \frac{100(100+1)}{20+1} = \frac{10,100}{21} = 481.0,$$

\hat{K} could actually vary from

$$\hat{K} = \frac{100(100+1)}{13+1} = \frac{10,100}{14} = 721.4$$

down to

$$\hat{K} = \frac{100(100+1)}{29+1} = \frac{10,100}{30} = 336.7.$$

Multiple Samples Taken (Schnabel's Procedure)

For some time, the original attempts to estimate population density by marking involved just two samples, but subsequently the methods of LaPlace and Dahl were extended to cover numerous samples taken over a longer or shorter period of time and in many different circumstances. As a result, a voluminous literature has arisen on the subject, and has been augmented practically every month to the present time. To date, the best general review of the multiple sampling procedures was given by Ricker (1958:100-144), and his work should be consulted for further details. The papers by Chapman (1952, 1954) and Schaefer (1951) are also of unusual value in this regard.

The assumptions required now are the same as those for only two samples. Multiple marking and sampling can still yield estimates of population abundance even when recruitment or immigration causes change in the fraction of the population marked, but the details of the adjustments which must be made are beyond the scope of the present paper; the interested reader is referred again to Ricker. According to Ricker (1958:100), beginning in the 1930's several workers were known to have used repeated marking and recapture or reobservation, that is, multiple samples; but apparently the first of these to publish the theory of the method was Schnabel (1938). It turned out that her procedure was only a slight, although important, extension of Dahl's (1917) formulation and was as follows:

$$\hat{K} = \frac{\sum (X_i \cdot X_m)}{\sum X_{i,m}}$$

As before, \hat{K} is the estimate of total population, but the remaining symbols have been modified slightly; X_i are the animals captured on the i^{th} occasion, that is, on any given occasion one wishes to consider; X_m is the total number of animals that have been previously marked and released alive, that is, those marked successfully in the samples X_1, X_2, \dots, X_{i-1} ; and $X_{i,m}$ is the number of animals in the (i^{th}) sample which bears marks.

As was true of LaPlace's and Dahl's original procedure, the above expression was discovered by biometricians to be slightly biased, the more so as the number of recaptures became smaller. Therefore, for large populations several corrections were proposed, of which Chapman's (1952) adds 1 in the denominator.

Although the adding of 1 in the denominator of Schnabel's original expression may seem like only a slight change, it leads to relatively large differences in estimates of the total population, \hat{K} ; especially when the sum of the number of recaptures, $\sum X_{i,m}$ is less than, say, 50 or 60.

It must be remembered that, in the multiple capture procedure, the number of captures on each given date, X_i , must be multiplied by the number of animals marked prior to that date, X_m . Then each of the resulting products must be summed cumulatively down through the last date when a sample was captured.

Let us consider the following example: Suppose that 50 mice were caught, marked and released on a given date, the first of a series of samples; on the second date, 40 mice were caught of which 11 were already marked; and on the fourth date, 60 were caught of which 20 already bore marks; following this, the work was stopped. Of course, on the first three dates, any animals not bearing marks when first noticed in the traps were immediately marked before they were released. A table of the data and some resulting computations would look as follows:

Sample Number				
1	0	50	0	0
2	50	40	2,000	8
3	82	35	2,870	11
4	106	60	66,360	20
Σ	—	—	71,230	39

Therefore, the Schnabel estimate (with Chapman's modification) for the total population was

$$\hat{K} = \frac{71,230}{39 + 1} \doteq 1,781.$$

Schumacher and Eschmayer (1943), Chapman (1948, 1954), and DeLury (1958) gave formulas for the variance, and Ricker (1958:102-103) has nicely illustrated the use of some of them. However, calculating the confidence limits for the Schnabel-type estimates of population density, by formula, is somewhat tedious and so will not be discussed here.

Fortunately, Chapman (1948) has provided a table that approximates the confidence limits where the ratio of marked to unmarked animals is small and the distribution of marked animals can thus be approximated from the Poisson distribution.

Within the body of Chapman's table, reproduced here as Table 1, he gave the upper and lower bounds, at the 95% confidence level for the ratio $K / \sum (X_i X_m)$; and he has set these bounds opposite to appropriate values of $X_{i,m}$. We notice that since Chapman's table shows the confidence limits for the ratio $K / \sum (X_i X_m)$, it is easy to "plug in" one's own observed values by multiplying the product $(X_i X_m)$, from the last line of the data in a Schnabel table, times the lower bound which was read off from Chapman's table. This is equivalent to cancelling the denominator of $K / \sum (X_i X_m)$ and leaves just K , or that is in this case the estimated smallest total number of animals on the study area. The same procedure would be repeated for the upper bound shown in the table, and it would give the upper bound for K .

In the hypothetical example shown above, the last line of the Schnabel-type table gave a sum of 39 animals which were found to bear marks when recapturing was done. Therefore, one would enter Chapman's table, Table 1 of this report, where $X_{i,m} = 39$, for which the ratio $K / \sum (X_i X_m)$ has limits of .01805 and .035. Multiplying the latter two fractions times the sum of $(X_i X_m)$ shown in the last line of the example, that is, 71,230, one gets about 1,282 and 2,493; these are, therefore, the upper and lower limits at the 95% confidence level for the number of mice that was estimated in the example above to be 1,781.

As the sum of the recaptures increases, the confidence limits narrow rapidly because the Poisson distribution is less skewed as sample size increases. Although, as can be seen, the original table extended only to a total of 50 recaptures, large-sample theory based on the z -distribution could be used for totals larger than 50, as Chapman (1948) pointed out. That distribution would provide an approximation to the binomial distribution, where the fraction of the total captures that bore marks is considered the mean of the binomial events, but the interested reader should consult statistics textbooks for a review of this.

Many other developments based on marking have occurred. In fact, Ricker (1958:81-83) showed that four major methods and two or three variations of each are available for estimating population density by marking. "Point" sampling, or "Jackson's method" is a major variation that will now be mentioned briefly.

During the preceding discussion, it was implicitly understood that the population was closed, that birth, or death, or migration, or some combination of them did not occur in the time between samplings; or, if one or more did occur, they did not change the

TABLE I.

95 Per Cent Confidence Limits for $K/X_1 X_m$

X_{1m}	<u>Lower Limit</u>	<u>Upper Limit</u>	X_{1m}	<u>Lower Limit</u>	<u>Upper Limit</u>
0	0.0885	-----	26	0.02478	0.0563
1	0.0720	19.489	27	0.02408	0.0539
2	0.0767	2.821	28	0.02342	0.0516
3	0.0736	1.230	29	0.02279	0.0495
4	0.0690	0.738	30	0.02221	0.0475
5	0.0644	0.513	31	0.02165	0.0457
6	0.0600	0.388	32	0.02112	0.0440
7	0.0561	0.309	33	0.02061	0.0425
8	0.0526	0.256	34	0.02014	0.0410
9	0.0495	0.217	35	0.01968	0.0396
10	0.0468	0.188	36	0.01925	0.0384
11	0.0443	0.165	37	0.01883	0.0372
12	0.0420	0.147	38	0.01843	0.0360
13	0.0400	0.133	39	0.01805	0.0350
14	0.0382	0.121	40	0.01769	0.03396
15	0.0365	0.111	41	0.01733	0.03300
16	0.0350	0.1020	42	0.01700	0.03210
17	0.03362	0.0945	43	0.01668	0.03124
18	0.03233	0.0880	44	0.01636	0.03043
19	0.03114	0.0823	45	0.01606	0.02966
20	0.03004	0.0773	46	0.01578	0.02892
21	0.02901	0.0729	47	0.01550	0.02822
22	0.02806	0.0689	48	0.01523	0.02755
23	0.02716	0.0653	49	0.01498	0.02691
24	0.02632	0.0620	50	0.01475	0.02625
25	0.02552	0.0591			

I am grateful to Dr. Chapman for permission to reprint this table.

tag ratio (of marked to unmarked animals.) However, the "point" sampling method contains refinements that can be used to estimate density even when extraneous changes do occur, and also the method permits estimates of birth and survival rates. The general approach seems to have been originated mainly by Jackson (1936; 1939) while analyzing a population of tsetse-fly (*Glossina morsitans*). However, the work was immediately, or perhaps concurrently, expanded in the "trellis diagram approach" by Dowdeswell, Fisher and Ford (1940), because the latter authors state (p. 131) that, "The theory of the interpretation of recapture frequencies has been gradually developed in collaboration with Dr. C. H. N. Jackson for many years during his researches on the tsetse fly in Tanganyika territory," and, moreover, Jackson in his 1939 paper (p. 246) acknowledges the "invaluable help" of Prof. R. A. Fisher and Mr. W. L. Stevens.

Two main variations were published by Jackson: In the first, called the "positive method," one short period of marking is done, but a number of periods of recapture take place; in the "negative" method, marking is done on a number of dates but recaptures are made on one date. Andrewartha (1961:26-34) discussed the method, including the trellis diagram and illustrated with detailed examples (pp. 202-210). The explanation of the "point" sampling method of estimating population density, given by Jackson (1939) himself, is fairly clear, and the brief treatment in Dowdeswell, Fisher, and Ford (1940) is commendable. Numerous others have studied the method and their contributions are evaluated by Chapman (1954).

In the present relatively brief review of a huge field, it is intended only to indicate some of the main developments, and therefore, the equations for the "point" sampling techniques will not be mentioned, particularly since the procedure necessarily becomes somewhat "messy" and involved. However, the following may indicate a general line, without regard to any specific publication, that can be followed to go around the problem of deaths, births, and other factors which change the tag ratio.

As is well known, one can estimate mortality and survival rates in a stationary population by (a) marking a cohort of animals in a very brief period, (b) capturing successive samples at later times in the future, in order to study change in the tag ratio as the marked animals die out and are replaced by

unmarked ones, and (c) calculating the rate of mortality in these marked animals from the change in tag ratio. (This or something similar is commonly done in constructing an age-specific life table, for example.) Knowing the rate of decline in the marked component and its rate of replacement by unmarked animals, one can then calculate how many marked animals should have existed on some prior date if a given number exists now. This same idea of projecting backward can be used when the decline in marked animals is due to egress from the area, or when it is due to a combination of death and egress. Thus a corrected number of recaptures can be derived and the total abundance estimated, all in spite of the fact that the tag ratio was changing as sampling continued over a fairly long period of time.

In brief summary, the marking methods are extremely valuable and consequently widely used. Fortunately, the estimators do not require the data to form any specific distribution, although the confidence limits for the models require specific distributions of data. The biological problems are, as usual, more acute than the statistical ones, and eventually they tend in many cases to violate the assumptions on which the models rest, especially when multiple sampling is used and longer periods of time go by. Changes in the animals' behavior cannot readily be compensated for by statistical refinements, and herein lies the principal shortcoming of the marking methods, the tendency for the animals to become trap-prone, net-shy, etc. Moreover, many man-hours of work and much expensive trapping material are often required to catch and mark the animals, especially among the keen, mobile ones such as the mammals and birds. If a net can be used to strain the animals out of an aquatic or gaseous medium, or better yet, if the animals can be attracted to a light as in the case of many insects, the cost of the marking methods can be much reduced. Regardless of the problems, the investigator will often be well advised to estimate the density of his specific populations by several methods, including this one, to determine the amount of agreement among the estimates.

ESTIMATING POPULATION DENSITY BY THE REMOVAL METHOD

Introduction

"Removal methods" of estimating density are evidently much newer than those based on marking, because, according to Davis (1963:103), they were first used in 1914 in Norway on bears by Hjort and Ottestad (see Hjort *et al.*, 1933). Leslie and Davis (1939) also published the method, theirs being the first well known report on this procedure. According to a valuable discussion by Ricker (1958:145), a number of other workers published reports on the technique in several countries as early as the 1940's, but not until DeLury (1947) refined the procedure did it come into common use in fishery ecology. Moran (1951) derived maximum likelihood equations for estimating density by the removal method, but his procedure is a special case of DeLury's (1947) more general method, according to Zippin (1956). Methods for finding the confidence limits were presented by DeLury (1951), Chapman (1955), Zippin (1956, 1958) and others.

During each year additional publications on the removal method are appearing, and already the literature on the subject is growing heavy although it has some way to go to equal the work on the marking procedures. Fortunately, the report of Hayne (1949a) and the reviews by Davis (1963:103-117), Ricker (1958:145-184), and Chapman (1954, 1955) are excellent, and they should be consulted for details. The reports by Zippin (1956, 1958) also give syntheses valuable for both biometrists and practicing ecologists. Southwood (1966:174-186) briefly reviewed removal methods, including how the data might be obtained among insect populations. Recently, Rupp (1966) has simplified the field by showing that the removal methods and tagging methods are, in principle, special cases of one and the same scheme.

The underlying theory of all the removal methods for estimating population density is that removing a known number of animals will cause a measurable change in some quantity that can be determined by sampling. Some of the principal variations on this theme are: (1) number of removals on each given date (per unit of effort, i.e., per day, per trap-night, etc.) compared to total previous removals, (2) comparison of number of re-

movals (per unit of effort) on successive dates, (3) the amount of change in the observed sex or age ratio caused by a known amount of removal, or (4) the amount of change in the number of one species compared to another caused by a known amount of removal, etc. Many other possible ratios can be studied from the standpoint of their change resulting from a known amount of captures (and removals).

The first two general methods are closely similar to each other and the only applicable difference is whether the periodic catch shall be summed cumulatively or considered separately in the individual samples. The third method, involving change in sex or age ratios, at first thought appears much different, but, as was brought out by several writers (for example, Davis, 1963:106), the general idea is closely similar to the other removal procedures; the principal point of departure is that the animals need not be captured to obtain ratios if the various sex, or age, or other components can be distinguished in the field and the animals are removed only once.

Other developments included Hayne's (1949a) proposal that the periodical catch be plotted on the Y-axis against the cumulative catch on the X-axis and the results be analyzed by regression methods; the point where the curve intercepted the X-axis would indicate the estimated total population. In addition, DeLury (1951) made the valuable suggestion that the removal method and the marking method should be used at the same time; animals should be trapped alive, marked, released, and some would be captured again, but any that bore marks would be considered "dead" mathematically. Thus, successive captures would have fewer and fewer unmarked animals due to the mathematical (but not real) removal of marked ones. Chapman (1955) also considered the combination of tagging and removal work in one study.

Assumptions and Data

The usual assumptions on which the removal methods rest were covered by, among others, Ricker (1958:151-152), Davis (1963:105), Zippin (1956), and Chapman (1955); and Zippin condensed them down to three main ones:

1. The population must be essentially stationary during the period studied, except for the change caused by the investigator's removal; that is, births, deaths, immigration, and emigration do not occur, or at least, their effects cancel

out. However, Lander (1962) and Chapman and Murphy (1965) have shown that these problems are much lessened when one is estimating density with what the latter call "survey-removal" methods, i.e., those involving removal with associated change in sex or age ratios, etc.

2. The probability of capture (or removal) is the same for each animal.
3. The probability of capture (or removal) for any given animal is the same during each different period when capturing (or removing) is done.

To these I would add:

4. In all but the survey-removal methods, the unit of effort during successive removals must be approximately constant.

As the authors mentioned above and other workers pointed out, the assumptions are frequently not fulfilled, especially when the removal is carried out over a long period of time. The longer the period of time that has elapsed, the more that animals from outside of the area of study are likely to move in and take over the home ranges of animals that man has removed; the mathematical removal of live (tagged) animals that are returned to the population tends, however, to overcome the problem of ingress, inasmuch as the animals' home ranges obviously do not become vacant when the animals are returned alive to the general population. Also, the longer the time between surveys, the more likely that the population abundance will change due to births and deaths, and the more likely that the behavior of the animals will also change.

A peculiarly bad problem with removal methods is the change in "catchability" of the animals, since, of course, those animals that are most accessible, most favorably inclined toward the trap bait, least wary, etc., will tend to be removed first; and the longer that the netting, trapping, fishing, or shooting goes on, the more difficult it will be to capture the average animal still remaining at large.

The amount of effort expended by the investigator during successive removals is probably often not the same. Even though the trapper (netter, hunter, etc.) may put in the same number of hours on each period or removal, he may work harder during some than during others, or his work may gradually become more efficient as he continues, resulting in higher catches of animals in relation to the number then present. In the survey-removal variation, usually only one removal is made, and of course then variations in effort or variations in probability of

capture are not harmful.

Inconstant susceptibility of the animals to the capturing technique is the largest potential source of error, according to Ricker (1958:151), for most of the removal techniques. As usual, we should estimate population density by a variety of methods and compare the results to better judge the reliability of the several estimates.

To sum up the bases on which removal procedures rest, one finds that two main comparisons may be made among the "removed" elements: (a) current removal from the population at large as compared to previous removals, or (b) removal of some restricted natural segment of the population, such as a sex or age class, compared to removal of some other class. Concerning removal among the population at large one may have (1) actual removal or (2) marking and replacement of live animals that are treated mathematically as dead. The resulting estimates of the population will obviously be made by either (a) plotting the data on graph paper and drawing the best linear regression line obtainable from gross visual inspection or, preferably, from fitting the line by the least squares method; or (b) by solving various formulas, collectively called "multinomial methods." From the standpoint of analysis, actual removal and mathematical removal of animals drawn from all of the components of the population can be handled by the same models, whereas the techniques requiring a selective removal of some restricted component of the population (as a sex or age group) require somewhat different approaches, especially inasmuch as only one removal normally occurs in practical work.

Current Removal Relative to Previous Removal

Regression — The number of animals removed on a given date per unit of effort, or per cumulative total of animals previously taken, etc., yields one point on a graph. When the same work is extended over several dates, successive points in a scatter diagram can be drawn. It is straightforward and relatively simple, to calculate the line of best fit, based on the well-known least-squares regression. The formulas for linear regression are given in textbooks of statistics. Let it be supposed that one plots the number of animals successively removed (either actually or mathematically) per unit of effort against the total number of animals previously removed. Let it be understood that the number caught per unit of time, such as per trap night, will be the dependent variable Y and the total number of animals previously caught will be the independent variable X . (The "unit of effort"

must be closely controlled or large errors will result.) Then, in the standard terminology of regression methods (see for example, Snedecor, (1956:123-125),

$$\hat{Y} = b(X - \bar{x}) + \bar{y},$$

where \hat{Y} is the best-estimated value of Y as defined above; \bar{y} is the average of the Y 's, that is, the average number of animals captured per unit of time; \bar{x} is the average of the X 's, that is, the average of the cumulative total number of animals captured during the entire period. Regarding the latter, consider, for example, that 25 animals were trapped the first night, 21 the second night, 18 on the third, and 12 on the fourth. The cumulative totals are, respectively 25, 46, 64, and 76, for which the average, \bar{x} , would be 53. To continue, with the symbols, the symbol b is defined by

$$b = \Sigma xy / \Sigma x^2,$$

where x is the deviation of X from \bar{x} and y is the deviation of Y from \bar{y} . b is called the regression coefficient; it gives the slope of the regression line, because for every change of 1 unit in X , there will be a change of b units in Y . Thus, the line of best fit can be calculated and drawn; where it crosses the abscissa will be the estimated total population of the area sampled. In addition, and this is rather important, confidence limits for the fitted regression line can be rather easily found from the equations given in the many books of statistics.

Multinomial Methods — When the animals are removed from the population at large, either actually or mathematically, and this is done only twice, the population density may be estimated from the simple relationship (Zippin, 1958) :

$$\hat{K} = \frac{Y_1^2}{Y_1 - Y_2}.$$

As usual, \hat{K} means the estimated total number of animals present, Y_1 is the number removed during the first period of capture, and Y_2 is the number removed during the second period of capture. If the animals are removed during exactly three, four, five, or seven periods, the total size of the population may be rapidly calculated with the aid of charts, given by Zippin (1956, 1958), based on maximum likelihood equations.

In actual practice, the investigator would seldom use more than seven periods of removal, because by then the remaining (nonremoved) population would have become so small that additional efforts would tend to be unproductive and also because enough data would already have been obtained. However,

if one still wants to conduct more than seven periods of removal, the maximum likelihood equations provided by Zippin (1956, 1958), based on Moran (1951), can be used. As can be seen from Zippin (1958), the following "nasty" expression must be solved for $1 - q$, the probability of capture:

$$\frac{(1 - q) y_1 + (2 - q) y_2 + \dots + (n - q) y_n}{y_1 + y_2 + \dots + y_n} = \frac{q}{1 - q} - \frac{q^n}{1 - q^n}.$$

Here y_1 is the number of animals removed on the first occasion, y_2 is the number removed on the second occasion, etc. up through the n^{th} period or removal; and q is the estimated probability that an animal will not be captured (and removed). $1 - q^n$ gives the probability that an animal will be captured after n attempts (since $p = 1 - q$). Finally, the estimated

total population \hat{K} equals the total catch $\sum_{i=1}^n y_i$ over the probability of capture, thus:

$$\hat{K} = \frac{\sum_{i=1}^n y_i}{1 - q^n}.$$

The question comes up, when using the removal method, is it better to estimate population density by plotting the data and calculating the regression or is it better to use Zippin's charts and/or multinomial equations. Zippin (1956, 1958) analyzed this question rather thoroughly, and he concluded (1958) "a least-squares regression gives estimates that are as good as multinomial estimates; however, this method requires considerably more time to calculate than the multinomial estimate made using the graphs. The regression method may be recommended when the graphs are not available."

In my judgement, if more than two periods of capture are used, the best all-around procedure for most workers will be to calculate the regression from the well-known equations because (a) most workers are already familiar with the technique of calculating regression lines; (b) most workers have access to desk calculators, and consequently the time needed to perform the arithmetic is negligible, especially in relation to the time required to obtain the data; and (c) it is easier to calculate the confidence limits of a regression line by the familiar methods than it is to calculate the limits from the maximum likelihood equations of Zippin (1956).

Survey-Removal Procedures

Removal methods that involve unequal capture of two or more segments of the population and thereby cause a change in sex, or age, or other ratios have proliferated in recent years, although the procedure seems to trace back to the important papers of Kelker (1940, 1944). The statistical theory underlying the field has been developed by Chapman (1955) and Chapman and Murphy (1965), and other aspects were reviewed by Hanson (1963).

Among the many survey-removal procedures, one will now be briefly described to illustrate the general field. This one compared unequal numbers of males and females, but the theory can be extended to many other situations (Davis, 1963:106). Two randomized field surveys are made, one before the period of removal and one afterward, and the surveys yield the sex ratio of the animals during the pre- and post-removal times. Next, one must obtain a total count, i.e., a census, of all removed animals of each sex, or age group, or other components being compared.

Kelker (1940, 1944), Rasmussen and Doman (1943), and Petrides (1949) have published valuable survey-removal procedures for analyzing the situation where two segments of the population are removed, all of which were compared by Hanson (1963:53-58). However, since the method of Petrides (1949) seems a little easier to understand, it will be reproduced here, as follows. It is assumed that the ratio studied does not change except due to man's removal. Two proportions are established, as follows:

$$\begin{array}{rcl}
 \begin{array}{l} \text{Total Number of Mature Males,} \\ \text{in } \textit{Preremoval} \text{ Population} - \\ \text{Total Number of Mature Males} \\ \text{Removed} \end{array} & & \begin{array}{l} \text{Relative Number of Mature Males} \\ \text{in } \textit{Postremoval} \text{ Sample} \end{array} \\
 (1) \quad \frac{\quad}{\quad} & = & \frac{\quad}{\quad} \\
 \begin{array}{l} \text{Total Number of Mature Fe-} \\ \text{males, in } \textit{Preremoval} \text{ Popula-} \\ \text{tion} - \text{Total Number of} \\ \text{Mature Females Removed} \end{array} & & \begin{array}{l} \text{Relative Number of Mature} \\ \text{Females in } \textit{Postremoval} \text{ Sample} \end{array}
 \end{array}$$

$$(2) \quad \frac{\begin{array}{c} \text{Total Number of} \\ \text{Mature Males, in} \\ \text{Preremoval} \\ \text{Population} \end{array}}{\begin{array}{c} \text{Total Number of} \\ \text{Mature Females} \\ \text{in Preremoval} \\ \text{Population} \end{array}} = \frac{\begin{array}{c} \text{Fraction of a } \textit{Pre-} \\ \text{removal Sample} \\ \text{Composed of} \\ \text{Mature Males} \end{array}}{\begin{array}{c} \text{Fraction of a } \textit{Pre-} \\ \text{removal Sample} \\ \text{Composed of} \\ \text{Mature Females} \end{array}} \times \frac{\begin{array}{c} \text{Total Number, of All} \\ \text{Sexes, in } \textit{Preremoval} \\ \text{Population} \end{array}}{\begin{array}{c} \text{Total Number, of All} \\ \text{Sexes, in } \textit{Preremoval} \\ \text{Population} \end{array}}$$

The foregoing concepts in the word equations will now be symbolized as follows: A_B , total males in population, before removal; E_B , total females in population, before removal; A_G , total males removed; E_G , total females removed; M_B , number of males in sample, before removal; F_B , number of females in sample, before removal; M_C , number of males in sample, after (at completion of) removal; F_C , number of females in sample, after removal; U_B , total number of all sexes, in whole population, before removal; and N_B , number of animals of all sexes, in sample, before removal. Therefore, the two basic proportions of Petrides (1949) were

$$\frac{A_b - A_d}{E_b - E_d} = \frac{M_c}{F_c},$$

and

$$\frac{A_b \cdot \frac{M_b}{N_b} \cdot U_b}{E_b \cdot \frac{F_b}{N_b} \cdot U_b} = \frac{M_b}{F_b}.$$

It is obvious that M_b / N_b gives the fraction of a sample which is composed of males before removal and that F_b / N_b gives a comparable fraction for females. After the two major proportions of Petrides given above are solved simultaneously by the usual methods, they will yield U_b , the total number of the entire population before the removal began. In the process, the worker eliminates from the first proportion the unknowns A_b and E_b by putting into the first equation the equivalent expressions shown on the righthand side of the second equation. The final result gives:

$$U_b = \frac{N_b (A_d F_c - E_d M_c)}{M_b F_b - M_c F_b}.$$

Variance When Population Closed. — Formulas for the asymptotic (large-sample) variance of the abundance (estimated from survey-removal methods) were developed by Chapman (1954, 1955). Apparently, many ecologists are not aware of his variance formulas for the survey-removal estimates, perhaps partly because Chapman's two articles were published in journals of theoretical statistics and written in a technical mathematical style. Unfortunately, Hanson (1963) overlooked both of these important papers; and although Davis (1963:103 and 114) cited both of the papers by Chapman, he said (p. 106) in his excellent review that no estimate of variance was available for the "sex ratio method" (survey-removal procedure).

The asymptotic variance of the population's estimated abundance before the removal began, $\sigma^2(\hat{N}_0)$, was given by Chapman (1955) as

$$\sigma^2(\hat{N}_0) = \frac{\frac{X_0 Y_0}{n_0} + \frac{X_1 Y_1}{n_1}}{(P_0 - P_1)^2}$$

The symbols used above are those of Chapman and have the following meanings: First, the subscript "0" refers to the beginning of a period of time, that is, to the time when the first of a pair of field surveys is made; the subscript "1" refers to the end of this time period, or the occasion of the second survey, made after the removal was over (and of course the subscript "i" is a general description meaning here "any given time selected"). X_i and Y_i are the size of classes X and Y at times t_i , and the two classes combined make up N_i , the total population at time t_i . P_i is the fraction of the total population made up by a given class; that is, $P_i = X_i / N_i$; and n_i equals the size of the i^{th} sample. X_i and Y_i would have to be replaced by their expectation, the estimates previously derived from the equations of Kelker (1940, 1944) or ones similar to them, such as Petrides' (1949) discussed above, since obviously the true size of any given population component would not usually be known.

Estimates When Population Not Closed. — Most workers using the survey-removal techniques of estimating population density have assumed that the population ratios did not change appreciably in the time between the field surveys except due to man's removal. In other words, either the population was closed or,

if not closed, the extraneous factors were not appreciably changing the ratios investigated. Although most populations, of course, suffer natural mortality, have members moving into and out of the population, and experience other changes, nevertheless it is reasonable to believe that most of these factors do not usually change the ratios enough to cause any large amount of error, particularly if the time between surveys is reasonably short. Certainly, compared to sampling errors, these other potential errors should be small. If the investigator has good reason to believe that his assumption is not being met, he might shift attention to other population parameters; perhaps sex ratios instead of age ratios, for example.

Lander (1962) considered methods for estimating the rate of fishing or other removal by man based on, he said, "knowledge of catch and of the change in composition caused by selective removal of one class during the catch interval." Lander continued, "From a mathematical viewpoint it [the paper of Lander] simply shows how Chapman's (1955) fundamental work relates to the theory of fishing as developed by authors like Ricker (1958) and Beverton and Holt (1957)." Among other things, Lander presented a model which yielded the "fishing rate" even where natural mortality occurred in the time between surveys. He concluded that unequal rates of natural mortality directed at the classes studied "may not be serious in practice," especially when the class whose rate of capture was being estimated also suffered a higher rate of natural mortality than the other class. Lander presented considerable theoretical material but developed the mathematics clearly in easy stages. Although Lander's paper dealt mainly with estimation of capture rates, it contained much of value on estimating population abundance, since, of course, once the rate of capture is estimated, the actual number of animals caught can be divided by the rate to give the estimated abundance.

Chapman and Murphy (1965) gave several models for estimating population density under several different conditions of an open system and gave their variances. Besides deriving the instantaneous rate of fishing or other removal by man, where the instantaneous rate of natural mortality on the X class, M_x , equals that on the Y class, M_y ; they also developed the more interesting case where the natural mortality rates of the classes were different. To accomplish the latter, they invoked again the idea of amount of effort spent on the capture. In other words, when the classes had unequal natural mortality, Chapman and

Murphy inserted factors in their models to take account of removal rate per effort expended and combined this with parts of the standard survey-removal theory. After some comparatively elaborate mathematics, they finally obtained an approximation to the instantaneous rate of natural mortality for the case of a continuous removal ("a constant level fishery," etc.). However, Chapman and Murphy concluded that the estimates of the capture rates "are essentially independent" of the natural mortality rates, and "Furthermore, it is reasonable to believe that if M_x and M_y are not too widely different and are small relative to F_x , again a common fisheries situation, the estimate of F_x will not be appreciably affected by the inequality of M_x , M_y ." (F_x is the instantaneous rate of removal by man, in the notation of Chapman and Murphy, and M_x and M_y are the instantaneous rates of natural mortality on the X and Y classes, respectively.)

The report by Chapman and Murphy (1965) contained considerable discussion of the assumptions involved in their models and gave variances, and for these and other reasons it is a valuable contribution. Unfortunately, since the equations were developed in a terse mathematical style, with little discussion or explanation, the report tends to be obscure.

Similarity of Survey-Removal Methods and Marking Methods

Rupp (1966) has pointed out that many methods of population estimation based on the changes in abundance of one class relative to another have an underlying common basis and, in fact, are identical if it is understood that the symbols for the classes which are compared can be positive or negative, depending on whether animals are added to or removed from the population. In the case of marking experiments, the marked animals can be considered, in one sense, a new group that has been added to existing components.

After giving the usual assumptions, Rupp defined symbols similar to the following:

N_i = population size at time i .

1,2 = subscripts showing the beginning and end of period studied ($i = 1,2$).

p_i = decimal fraction of population in a selected class, such as M, at time i .

M, F = actual number of animals added to or removed from a selected class compared to a contrasting class, such as, respectively, males and females.

Furthermore, and this is important, Rupp required that M and F could each take on positive or negative values accordingly as the animals were added to the population or removed. As usual, p_1 had to differ from p_2 as a result of the addition or removal.

Rupp then wrote two basic equations:

$$p_2 N_2 = p_1 N_1 + M,$$

and

$$N_2 = N_1 + M + F.$$

The first equation implies on its left side that the number of the total population, at the end of a period of study, composed of a selected class such as M equals the number that it composed at the beginning plus the number M added (or removed); one must remember that M can be positive or negative and, hence, one may be adding a negative number on the right. The second expression was substituted for N_2 in the first equation, and the result was solved for N_1 :

$$N_1 = \frac{M - p_2(M + F)}{p_2 - p_1}.$$

Rupp (1966) showed that the Dahl (1917) equation based on marking is a special case of the above equations where $p_1 = 0$. Let M now be the class bearing marks. Therefore, if $p_1 = 0$, it is implied that when the period of study began, no animals bore marks. Thus, in the initial equation of Rupp, $p_1 N_1 = 0$, and so

$$p_2 N_2 = 0 + M = M.$$

The latter equation can be rewritten as

$$p_2 = M / N,$$

and when R / M is substituted for p_2 , it gives finally the old familiar Dahl estimator $M / N_1 = R / M$. (R = the number of animals in the second sample which bear marks, and, hence, are recaptures.)

Rupp's (1966) formulation seems to contain one minor inconsistency (mostly just a matter of definition) where he said that N_1 could be assumed to equal N_2 when his equations above reflect "addition" of marked animals to the population. The difficulty is that the marked animals are treated as though they are actually added to the population, but of course they are ones already present that are simply converted to a marked status. Therefore, in the second of Rupp's two most basic equations, which was

$$N_2 = N_1 + M + F$$

if $N_2 = N_1$, as stated by Rupp, then some number of unmarked animals, that later becomes marked, designated by me as U , must be added to the left side of the equation to balance, where it is understood that $U = M + F$. This would, in a marking experiment, convert the last equation above to

$$N_2 + U = N_1 + M + F;$$

but since $F = 0$, then $U = M$, and the result is, as it should be,

$$N_2 = N_1 + (M - U) + 0$$

or

$$N_2 = N_1 + (0) + 0.$$

The same result seems to be achieved by a somewhat peculiar method in Rupp's equation (4) which is not well explained; perhaps the problem is mainly one of definition of symbols. Rupp (1966) points out that one component such as M could be "added" to the population (by marking) at the same time another component such as F is removed; in that case F would of course not equal 0 in the equations above.

Rupp's interesting report gives the same conclusion that a number of us heard expressed in a class in 1963 by one of the instructors, Dr. W. Scott Overton, now of Oregon State University; and possibly the idea has occurred to others. The report of Rupp bears out Dr. Overton's oral, and Davis's (1963:118) written, statement that many of the methods for estimating population density are essentially the same or closely similar, that in reality the population ecologist has few basic methods available, and that he needs more.

In summary, the removal methods may be considered from mathematical, biological, and economic standpoints, all of which interact to some extent. Simple yet sound removal models are available, and more are being developed. On the other hand, Zippin (1956) found that the precision of estimates based on removal per unit effort was relatively low. For example, if one wanted the coefficient of variation to be not over 20%, a rather low degree of variation for biological work, and if the true population size was 10,000, then 2,500 animals, or 0.25 of the population, were required to be removed. If the population contained only 1,000 animals, 0.45 of them would have to be removed. If the total population was smaller or if a higher degree of precision was required, an even higher fraction of the population would of course need to be removed. Further, as Zippin (1956) remarked, although it is normally assumed that the population is stationary and that the probability of capture is approximately constant, in fact both requirements are fre-

quently not met. However, in my opinion the need for a constant probability of capture can be relaxed a good deal, for if this probability lessens in some regular, systematic way, a suitable regression curve can still be fitted. In general, when numerous periods or removal occur, it is better to calculate the density by regression methods than it is to do it by formula, partly because the regression relation does not have to be linear. When mathematical rather than actual removal is used, the influx of new animals into vacated home ranges is lessened, and it is more economical to combine marking procedures with the removal ones. Survey-removal procedures, involving change in sex or age ratios or other relative numbers, rest on assumptions that can be more easily met than those of the marking category, according to Chapman (1955), but "... in almost all cases the capture-recapture estimation procedure will yield more information for the same amount of effort." In cases where hunters or fishermen carry out the removal the reverse should be true. In many species the survey-removal models of course cannot be used because no obvious sex or age or other distinction between the classes can be readily recognized in the field. The principal difficulty with the survey-removal methods is that the sex or age or other class of the population often exhibit different behavior, leading to unrepresentative samples from the field. If the removal is by shooting, a number of dead animals may be lost in the field, making the count of total removed animals wrong. In spite of these problems, the removal methods should hold much promise and should be investigated more. Menhinick (1963) got better estimates with them than he did with marking or with total counts on sample plots when he studied several kinds of insects. As usual, the worker should estimate density by several methods and compare results.

ESTIMATING DENSITY FROM STATISTICAL DISTRIBUTION OF DATA

Frequency of Capture

A newer group of methods for estimating population density of animals is that based on the frequency with which a recognizable given animal, or group of animals, is seen 1 time, 2 times, 3 times, etc. Of course, in most surveys, some of the animals will be seen 0 times, and the trick of the present class of methods is to estimate the size of this missing category. After the num-

ber of animals seen 0 times is estimated, the number can be combined with those positively known to be seen 1 or more times to give the estimated total. The present group of methods requires the investigator (a) to mark or otherwise positively identify individual animals and make repeated surveys to determine how often identifiable animals have been seen, (b) to decide what is the underlying distribution from which the truncated data are drawn and then (c) to estimate the size of the missing class either from the formula for the distribution or from regression methods. Some of the main variations based on frequency-of-capture involve (a) the type of distribution assumed, whether Poisson, negative binomial, geometric, or a logarithmic series; and involve (b) whether the models are maximum likelihood estimates or are moment estimates.

Craig's (1953) paper is the earliest on the subject seen by me and it was called to my attention by Dr. William Hovanitz. Hovanitz has told me that during his own research on butterflies he independently noticed the possibility of estimating the size of the missing 0 class with use of formulas for the Poisson distribution; he later asked Dr. Sewall Wright's advice on mathematical procedures that should be followed. Wright furnished a model; Hovanitz developed another. Hovanitz made all his data available to Craig who presented six models, of which Method 1 was due to Wright, Method 2 was Hovanitz's general approach and Method 5 was due to Stevens (1937).

To return from this little historical sidelight, the models derived by others and presented by Craig, and those due to Craig himself, are valuable contributions to the ever-growing literature on population estimation. In addition, to giving the density estimators, Craig (1953) furnished the variances for the six models, and illustrated with data on butterflies furnished by Dr. Hovanitz (and amply credited to him). The animals must be individually identifiable, requiring normally that they be captured, marked, released, recaptured, and so on, through as many cycles as possible. As usual, the captures must be at random. At once it can be seen that the frequency-of-capture techniques should be combined with marking work for the Schnabel equation; and, therefore, the remaining assumptions underlying the Schnabel approach would have to hold.

Craig (1953) concluded that, although the maximum likelihood estimators gave substantially the same results as did the moment estimators in trials on actual field data, "nevertheless with increasing sample size meaningful solutions of the likelihood equations do not exist." Therefore, I shall reproduce here Method 1 (of Wright) and Method 2 (of Hovanitz and Craig), both moment models and both requiring data from a Poisson distribution. Symbols of Craig, slightly modified, to fit the case where only two periods of capture are used, are:

r = total number of different animals captured.

x_i = class size showing number of times an animal was captured ($x = 0, 1, 2, \dots$).

$s = s_1 = \sum x_i f_i$ = total number of captures of the r animals = "first power sum".

$s_2 = \sum x_i^2 f_i$ = "second power sum".

f_x = number of animals caught x_i times.

n = animals existing in the whole population.

\hat{n} = estimate of n .

1,2 = subscripts designating the number of times a given animal is caught.

Method 1 is the equation:

$$\ln n - \ln (n - r) = s / n,$$

where \ln signifies of course the natural logs. The solution to the equation has to be iterative, by guessing a value of n , inserting it in the equation, and noticing how close the equation is to balancing. If not close enough, a new estimate of n is tried, etc. According to Craig (1953) the above equation can be "readily solved for the integer n which most nearly satisfies it by the use of a good table of natural logarithms," but in my experience the equation is difficult to handle.

Method 2, on the other hand, is simple to solve but gives coarse estimates; if desired, a trial value of n can be quickly found from Method 2 and inserted into the more exact formula for Method 1, as pointed out by Craig (1953). The equation for Method 2 is:

$$\hat{n} = s_1^2 / (s_2 - s_1).$$

Craig found the variance for "the proportional error of the estimate of n " by Method 2 to be

$$\sigma_{\hat{n}/n}^2 = 2n/s_1^2.$$

Craig showed the following example, based on Hovanitz's data on butterflies (*Colias eurytheme*):

x	f _x
0	—
1	66
2	3
<hr/>	
Σ	69 = r; s = 72.
$\hat{n} = 72^2 / (78 - 72) = 864,$	
$\sigma^2_{\hat{n}/n} = 2 (864) / 72^2 = 0.333.$	

That is, the variance was 1/3 of the estimate of n in this example, or very high, because only a small part of the population was sampled in that particular experiment.

Tanton (1965) estimated the population density of a mouse (*Apodemus sylvaticus*) by a frequency-of-capture model, devised by Brass (1958), and based on an underlying negative binomial distribution. As Tanton said, if the "catchability" of the animals had stayed the same throughout the population when the capturing was done, then a Poisson model would have been appropriate, but, since catchability varied, then the negative binomial was more suitable.

According to Tanton, his estimate was obtained directly from Brass's (1958) Method A. Although Brass said that his paper considered "simplified" methods of fitting the truncated negative binomial distribution, nevertheless the manipulation became fairly involved, particularly for estimating the variances. Tanton converted the observed number of animals captured 1, 2,...,n times to fitted numbers, derived somewhat laboriously, from which estimates of parameters were finally made. Further study of his data by Tanton indicated that the mice did not learn to avoid the traps, but nevertheless the probability of capture was not the same throughout the population. The accuracy of results from use of Brass's (1958) method seemed to be reasonably satisfactory to Tanton.

Eberhardt, Peterle, and Schofield (1963) and Edwards and Eberhardt (1967) also have developed methods for estimating population density from frequency-of-capture, but they assumed the population fitted the geometric distribution. The latter is similar to a negative binomial one; a succession of Bernoulli trials is conducted and the investigator estimates the probability that k failures precede the r^{th} success where $r = 1$; or to put it another way, the investigator estimates the probability that one success (the first one) would occur is $p q^k$ (Feller, 1957:155-156).

The paper by Edwards and Eberhardt discusses several methods for estimating population size by frequency-of-capture, based on a geometric distribution model, of which one of the most satisfactory ones was said to be derived from Hartley's (1958) procedure for maximum likelihood estimation where the data are incomplete and a truncated sample has resulted; Hartley mentioned that his approach was similar to the missing-plot technique used in analysis of variance. Several of Edwards and Eberhardt's methods involved plotting the capture frequencies and fitting regression lines. After Hartley's approach was somewhat altered by Edwards and Eberhardt (1967), the following maximum-likelihood estimate, based on the geometric distribution, was obtained:

$$\hat{N} = \frac{\sum n_x}{1 - (\sum n_x / \sum x n_x)}$$

The symbols above are those used by Edwards and Eberhardt and mean the following: $\sum x n_x$ = the total number of captures (without regard to how many of the captures represent animals caught once, or twice, or some other number of times); $\sum n_x$ = the total number of different animals captured; \hat{N} = the estimated total number of different animals in the whole population (or component studied).

Edwards and Eberhardt (1967) used a number of methods to estimate the abundance of cottontail rabbits (*Sylvilagus floridanus*) on two closely studied areas, including one a pen of 40 acres, and they found that the "geometric models" gave good results, particularly the equation shown above and a regression model. Multiple marking (with recapture) gave decided underestimates. Nixon, Edwards, and Eberhardt (1967) tested various procedures on several populations of tree squirrels (*Sciurus carolinensis* and *S. niger*) and concluded that both of the geometric models of Edwards and Eberhardt just mentioned gave useful results, whereas some procedures based on multiple marking (with recaptures) again yielded underestimates.

The proliferation of methods continues; appearing recently is a paper by Bennett (1957) giving a model rather related to the frequency-of-capture ones and yet not requiring the direct estimating of any missing class. Individual broods of ducks had to be identified during repeated sampling, and the number of

brood-sightings that were new were then plotted against the cumulative total of all previous sightings. After enough observations were made, said by Bennett to be reached when the ratio of new sightings to the cumulative total of earlier ones was near one-half, this gave a curve that tended to an asymptote. A logarithmic-series curve was fitted and the point estimated where enough total sightings would have been made to have yielded essentially the last newly observed brood. In effect, it appears to me, the size of the "zero class" is estimated indirectly at the point where it practically vanished; this is the point where nearly all of the unseen animals have been converted to observed ones. Confidence limits were not provided.

Relation of Variance to Mean

Hanson and Chapman (in press) have developed an estimator considerably different in principle from others discussed here because the method does not require that any population component be in effect positively identified by marking, removal, or total counts on sample plots (in principle an identification). On the contrary, rapid, cursory, incomplete counts are made repeatedly on an entire study area and the observed number of groups, and individuals within the groups, are recorded. Some convenient number, say 20 to 50, of rapid surveys are made under conditions as uniform as possible. The main assumption behind the procedure is that the data on number of groups for a binomial distribution, requiring among other things that each group will be seen or not, that the probability of observation is the same from group to group of animals and survey to survey, and that the observations are independent (clumping of groups not noticable). A secondary assumption is that the number of animals living on the study area remains nearly constant during the period of surveys.

It is well known that in a binomial distribution the product $k_g p_g$ is estimated by the mean, \bar{x}_g , where k_g is the actual total number of groups of animals living in the study area, p_g is the probability of observing them during cursory, incomplete counts, and \bar{x}_g is the mean number of groups seen. It is also well known that the binomial variance, $k_g p_g q_g$, is estimated by s_g^2 ; q_g is defined by $1 - p_g$ and therefore is the probability that any given animal will not be seen during the incomplete counts. The expression for the variance can be divided by the one for the mean,

$$\frac{k_g p_g q_g}{k_g p_g} = \frac{s_g^2}{\bar{x}_g},$$

which after cancellation of like factors and replacement of q_g by \hat{q}_g of course gives

$$\hat{q}_g = s_g^2 / \bar{x}_g;$$

from this it immediately follows that $\hat{p}_g = 1 - (s_g^2 / \bar{x}_g)$. Since $p_g k_g = \bar{x}_g$, and thus $k_g = \bar{x}_g / p_g$, the expression given for p_g in the preceding sentence is substituted into this latest equation to finally yield

$$\hat{k}_g = \frac{\bar{x}_g^2}{\bar{x}_g - s_g^2}.$$

Thus, a moment estimator of the density of the animal groups is established, and multiplication of the estimated number of groups, \hat{k}_g , times the average number of animals seen in each group gives an estimate of the total population of the study area.

Confidence limits for the above model, based on an approximation from the chi-square distribution, were derived by Dr. Chapman (Hanson and Chapman, in press). Both the confidence limits for the groups as well as limits for the individuals within the groups must be found and used jointly to find the upper and lower bounds for the estimated total individual animals on the study area. Although the equations for confidence limits are fairly easy to use, an adequate description of them would require more space than is practical in this review.

The model was tested considerably on laboratory populations of mealworms (*Tenebrio molitor*) (Hanson and Chapman, in press). In general, the method did not work very well, mainly because the mealworms had a highly contagious distribution, part of which was caused by the worms "piling up" in the corners of the pans; even the use of the number of groups, rather than merely of total individuals seen, did not seemingly permit a close enough fit to the required assumptions of the binomial distribution. When sample size was as big as 30 to 35, the results were of course better than in trials where only 15 or 20 counts were made. Since in nature groups of animals should tend to be distributed more at random than individuals are, the model may have use in some situations and should be tested further.

The estimator just reviewed can now be compared to the one of Seierstad *et al.* (1967) mentioned in the section on "Total Counts on Sample Plots." Evidently the models are the same or closely similar, although the one of Seierstad *et al.* does not show all of the steps in the derivation. Some of the main ways in which the Seierstad paper differs is that (1) the confidence limits appear to be derived differently (but further study by a statistician will be needed to clarify the point), (2) the model was designed to determine the efficiency of surveys giving total counts, (3) use of the number of groups to circumvent partially the problem of clumping was not mentioned, and (4) empirical testing of their model was not mentioned.

The only other sampling method known to the writer that yields estimates of density without requiring total counts, marking, removal, or other measures leading to positive identification of all of the animals in some group, is the flushing-count method of King (1937), which was revised and improved by Hayne (1949b). Although the procedure has many interesting and valuable features and has had considerable use, it will not be described further except to mention that it is based on (1) the number of animals that are seen to run or fly from the observer as he walks along a predetermined survey-line and (2) the average distance between (a) the observer and (b) the spots where the flushed animals are first seen. King's method is thus not based on the statistical distribution of data in the sense that other papers covered here have been.

Summary of Models Based on Fitting of Distributions of Data

The frequency-of-capture methods require that individual animals must be marked or otherwise made identifiable, and this necessarily causes many of the potential shortcomings of other methods requiring marking. The model based on the interrelations of the mean and variance is nearly unique because no component of the population need be captured, removed, or otherwise made identifiable, either individually or as a group (as happens in principle when total counts are made on sample plots), and thus the data can be gathered more easily. All of the models covered in this section suffer from the following difficulties: (1) Probability of capture or of field observation may not be the same for all of the animals or their groups; (2) population density may change during the period of study; and (3) the data obtained may not fit the assumed underlying distribution.

Southwood (1966:88-89) claimed that any of the procedures discussed in Craig require the animals to be exceptionally mobile "so that their chances of recapture are virtually random almost immediately after release," and thus he concluded that the methods have limited possibilities except for "large conspicuous flying or very mobile animals under certain circumstances." I do not regard his reservations as being entirely warranted, however, because the time between captures need not be any shorter than they are in the multiple marking scheme. When an animal is captured on a given day, marked, and released, its presence can be ignored for the remainder of that day if it should happen to be caught again, or it can be ignored for longer periods. This will give it sufficient time to distribute itself randomly within the population. In other words, all of the initial encounters with the various trapped animals during one day (or a small number of successive days) can be treated as one sample all caught at the same instant. This sample can be compared to all of the initial encounters on a later day (or small group of days). By initial encounters is meant the first capture of a given animal on a given day, regardless of how many times it has been captured on earlier days. In general, the collection of valid data for the frequency-of-capture methods should not any more difficult than it is for the Dahl (Petersen) mark-and-recapture techniques.

The prospects for getting the proper data to fit the (positive) binomial method of Hanson and Chapman (in press) seem least likely. Prospects are better for Hovanitz's model (Method 2 in Craig, 1953) based on the Poisson distribution. The required assumptions for the data are even more likely to be met by the negative-binomial procedure of Tanton (1965) and the geometric method of Edwards and Eberhardt (1967). However, all of the methods based on the statistical distribution of the data have been tested so little in the field that it is not possible as yet to say which has greater value, although the model of Edwards and Eberhardt appears to hold most promise. Nevertheless, if some day sound methods could be developed for estimating population density from rapid, cursory, incomplete counts of free-ranging animals, this would greatly lighten the labors of the population ecologist.

CONCLUSIONS AND SUMMARY

This relatively brief survey of the rather enormous literature on population estimation indicates that many procedures are available but all of them contain pitfalls. Evidently there is not a "best" way to estimate population density for animals in general, because each population is unique in theory and in actuality, and each estimating procedure has strong and weak points. Although each one given population has continuity in time, it varies more or less continually. Results from estimating procedures are importantly affected by the biology of the animals, especially their ecology with its changing environmental influences. Therefore, the investigator who needs to estimate density should have in his repertoire numerous procedures to meet the variable ecology of the animals. Moreover, if density in any one time-period and place is estimated by several procedures, the worker can determine if the results obtained are nearly the same. If they are not, the work should be repeated and possible additional procedures should be invoked.

Although a number of papers have been cited herein, many were considered only slightly, and many more valuable writings on the subject were not even mentioned, whether by accident or intent. Additional papers on the subject roll off the presses monthly or weekly, and some represent marked departures from older procedures. The trend toward more models and greater testing of them should continue, and it will bring slow but sure gains in one of the ecologist's most difficult jobs, the estimation of population density.

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IN THIS ISSUE

Origin of Autumnal "False Broods" in Common Pierid Butterflies	A. M. Shapiro	181
The Lepidoptera Research Foundation, Inc.		194
Polyctor Polyctor in Mexico	H. A. Freeman	195
Ecological Color Variation in Some <i>Argynnis</i> of the Western United States	W. Hovanitz	197
Natural Habitats	W. Hovanitz	199
Estimating the Density of An Animal Population	William R. Hanson	203

THE JOURNAL
OF RESEARCH
ON THE LEPIDOPTERA

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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Established in 1962

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA has now nearly completed six volumes. At the moment, the publication schedule is somewhat delayed due to an editorial mishap which has had no lasting effects and every effort is being made to bring publication up to the normal schedule.

An editorial team of Associate Editors is in the process of being organized to aid the general editor in the procuring and screening of manuscripts for the journal. It is hoped that we will have this team organized in time for the issuance of Volume 7 to appear shortly. In any event, such a team as will begin to function shortly will be subject to addition from time to time so that the journal will not only be representative of all branches of Lepidopterology but also all parts of the world. The general editor will be grateful to all for recommendations and comments from others.

The editor has from time to time been confronted with inquiries from readers of the journal concerning the desirability of organization of local meetings of Lepidopterists connected in some way with the Foundation. The Editor would appreciate the reaction of readers to this subject. It should be borne in mind that the Editor would not have the time to organize these local meetings but would be willing to aid their existence in any way possible, as he has done several times in the past.

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FIELD INVESTIGATIONS PRELIMINARY TO
LIFE HISTORY STUDIES ON THE
LITHOSINA-MIONA-CASTA COMPLEX
OF THE GENUS ANNAPHILA (NOCTUIDAE)

CHRISTOPHER HENNE

Pearblossom, California

THE FAMILIARIZATION OF THE SPECIFIC HOST PLANT adaptations of the Genus *Annaphila* by the author of this paper, as well as by other field observers over a period of several years, offered evidence of the possibility that the published statement in Rindge and Smith's revision, to the effect that the larvae of *Annaphila lithosina* Grt., are predaceous, was considered by many as highly problematical, (as noted by J. S. Buckett in a recent publication) and was considered as worthy of further investigation.

It had been observed by numerous field workers who have collected the adults of this species (Bauer, Buckett, Leuschner, Sala, Henne and others) that the moths were generally taken in close proximity to masses of boulder outcroppings with shaded or damp conditions, and often with a small stream or seepage in the immediate area. Typical of the flight pattern of most of the members of this genus, specimens are netted when on the wing with difficulty and require extreme dexterity as stated by Frank Sala in his article on "The Difficulty of Collecting *Annaphila*" (Sala 196-). The rapid flight is somewhat curtailed by temperature extremes, becoming lethargic during a sudden drop in temperature or seeking shade during an exceptionally hot day. The visiting of available flowers near their habitat occurs during ideal weather conditions and oviposition also requires similar conditions and usually results in an opportunity for the field observer to determine the specific host plant of the species.

Until recently attempts at observing females of *lithosina* ovipositing in the field proved unsuccessful.

A partial list of a few of the localities familiar to the author where this species occurs, and the conditions in which specimens were collected, are as follows, beginning with the most southern (as far as known) extent of its range:

1. Kern River Cyn., Greenhorn Mts., Kern Co., Calif. el. 1200' & 2200' (Leuschner, Sala, Henne) specimens taken in flight and resting.
2. E. Kaweah River (Mineral King Rd.), Tulare Co., Calif., el. 2200' (Henne) collected in flight and visiting *Montia* and *Gilia* flowers. Same locality at 3200' el. (D. Henne) collected while visiting moisture.
3. Del Puerto Cyn., Stanislaus Co., Calif., (Longford, Powell).
4. 3 mi. E. Auburn, El Dorado Co., Calif., el. 1000', one adult in flight collected (Bauer, Buckett, Gardner).

We did not have a clue during this interval as to the plant association of *lithosina*, although Bauer, Buckett and Henne concluded that it was a plant typical of damp, rocky invironments, an ecology observed in the localities where the adults have been taken.

An important field observation was then made by Oakley Shields, while carrying on *Mimulus* research at the Carnegie Experimental Gardens at Mather, Tuolumne Co., Calif., el. 4600'. In a marshy meadow adjoining the "Gardens" he observed a female *Annaphila miona* Sm. ovipositing on *Mimulus moschatus* Dougl. The author of this paper had collected a series of this species in the area a few days before and confined females, with a selection of the plants that seemingly offered the best possibilities of including the specific food plant, but the females failed to oviposit. Unfortunately, weather conditions prevented further field research at that time. Shortly after returning to Southern California a Special Delivery letter was received from Oakley Shields describing his observations. This was the first tangible observation we had been able to acquire on the plant association of the closely allied species *lithosina*, *miona* and *casta*.

Although it was not possible to return to Mather for further studies on *miona* following Shield's report, the author devoted a considerable amount of time the following year in studying the plant ecology of various localities in which *lithosina* had been recorded. The two Kern Canyon localities were searched for members of the *Mimulus* group. A species of perennial *Diplacus* was found in the shade of the huge boulders where *lithosina* adults had previously been taken. An examination of the young growth did not produce ova or signs of larval feeding and there were no adults observed on the wing at that time. The leaf structure of *Diplacus* is generally viscous and hard, particularly when

the plant is exposed to the sun's rays and the flower budding period is late, but the terminal leaf growth or buds in a shaded environment could possibly accommodate the young larvae. A further search for moisture inhabiting species of *Mimulus* in the area was unsuccessful, and not too probable, due to the usual rushing torrent of the Kern River. Further field research in this locality might prove *Diplacus* to be one of the established larval host plants. Note: *Diplacus* is placed in the Genus *Mimulus* in some botanical literature.

The next locality visited was the E. Kaweah River on the Mineral King Road, where both *Diplacus* and *Mimulus guttatus* occurs, and where, as previously stated, adult specimens of *lithosina* had been taken. Both *Diplacus* and *Mimulus* plants were examined for ova at various elevations. A few *Annaphila* spp. were observed on the wing, but they were not accurately identified. However, as a clump of *Mimulus* growing on a damp, rocky outcropping at the side of the road was approached in the vehicle, an *Annaphila* was flushed, and it was quite obviously a female *lithosina*. The plants were examined and three ova were found under the terminal leaves. Unfortunately, the resultant young larvae were lost during the extended field trip.

Personal communication with Dr. Jerry Powell on the plant ecology in Del Puerto Canyon, where a series of *lithosina* contained in the University of California Collection at Berkeley were collected, established the fact that *Diplacus* was observed near where the specimens were taken. A casual survey by the author in this area failed to locate any stream or moisture inhabiting species of *Mimulus*.

The primary purpose of the field trip to northern California was to attempt, not only to determine the life history of *lithosina* but also that of the closely related *castas*. Coincidentally, Wm. Bauer and J. S. Buckett were fortunate in arriving at a locality near the American River, 3.5 mi. E. of Auburn at the height of the adult emergence of *Annaphila lithosina*, which made possible the excellent ecological paper by Buckett (Buckett, 1966).

Thanks to their cooperation, the author was notified of the *lithosina* flight and availability of ova on *Mimulus guttatus*. Fisch. This locality was familiar to all of us from a previous scouting trip made the year before, at which time in comparing a typical terrain with other localities in which *lithosina* occurred, this locality offered possibilities for future success. Later that same year Bauer and Buckett collected a single specimen here. A subsequent report by a student entomology major divulged another colony,

15 mi. N. E. of Auburn, Placer Co., California. The following year the author and his wife found still another colony 6 mi. E. of Auburn, Placer Co., Calif., where ova were collected. These supplied additional specimens which will be utilized in future life history studies presently being illustrated in full by John A. Comstock.

J. S. Buckett is also planning further studies in this group on taxonomic details, including setal maps; further observations on their ecology, and possibly the discovery of a key to the origin of their relationship.

In a recent letter from Wm. H. Evans, who has also contributed a great deal of valuable knowledge to this genus of moths, he stated that he had listed *Mimulus* as a possible foodplant several years ago but discounted the possibility, due to the late blooming period, as most of the other species of this Genus feed exclusively on the buds and flowers.

It appears that *lithosina* has only been reported in the southern part of its range in early April; early May in the vicinity of the American River, and the latter part of June in Plumas Co. Further field research should determine whether the adult emergence coincides with the plant growth or is dependent upon variations in weather conditions, or both.

A possible explanation for the erroneous statement that the larvae of *lithosina* are predaceous, might stem from the fact that Prof. Harry S. Smith in collecting early stage wasp material at Sacramento on February 16, 1915 may have located the galleries in partially decomposed wood (stump or log). There are numerous species of Microlepidoptera larvae that feed upon the wax combs or pollen packs of Hymenopterous insects, and it is possible one of the predaceous species of Micros might exist in a habitat of this type, or another supposition might be that the larvae could also have belonged to a known species of predator representing a different Order of insects. A larva of *lithosina*, if there was a colony nearby, possibly entered the wood in close proximity to the wasp galleries, and Professor Smith assumed that the larvae he observed were of the same species. It was discovered during the laboratory rearing that *lithosina* larvae enter available partially decomposed wood and form their pupal cells therein.

Several attempts were made by the author to determine the host plant of the little known species, *Annaphilla casta*. Hy Edw. The few known records at the time for the occurrence of the adults, as stated by J. S. Buckett, and its restricted range contributed to the difficulty of visualizing a tangible habitat.

The possible clarification of Walshingham's type locality (Camp 9), by J. S. Buckett, led to an investigation of the area and adjoining Oakland, Douglas Co., Oregon in May, 1965. A lumber mill had depleted the natural growth throughout the immediate area and no likely spot where *casta* might occur was found. However, a more thorough survey with more time allowed, could most likely produce a more acceptable habitat for this species, particularly between this area and the coast.

The next investigation on this field trip was made to the McDonald Forest, N.W. Corvallis, Benton Co., Oregon in the company of Stephen Perkins. Through the cooperation of Dean Shumway, Biologist in charge, and following records of two adults of *casta* taken by Noel McFarland in 1963, a likely habitat was found within the Forest, where *Annaphila diva* occurred commonly visiting the flowers of a *Montia* sp. and also ovipositing on the same plant. Many specimens of this species were taken on the wing by Henne and Perkins and upon examination three specimens were found to be *casta*, which were difficult to distinguish on the wing from *diva* except for their larger size. Two more examples were observed by the author, which were assumed to be this species, hovering over a marshy glade surrounded by tall conifers, but unfortunately they avoided capture. Later knowledge of this species would undoubtedly have proved that the specific larval host plant occurs here in this type of habitat, and the specimens observed were females in ovipositing action.

Another locality that offered possibilities for the establishment of a colony was in the Coast Range, west of Portland, Oregon but no adults were observed by Perkins or Henne.

Plans to return to Oregon for further field research on *casta* were postponed when it was learned through Wm. Bauer and J. S. Buckett that Noel LaDue had taken specimens of *casta* at Plantation, Sonoma Co., California. This information was followed by intensive field work in this area by Henne, Bauer, Buckett and Gardner. Several adult females were taken by Bauer and Buckett in 1965 but on a return trip by all of us a few days later no specimens were seen. The many species of plants examined did not produce any early stage material.

The following year the author and his wife returned to this locality and one female *casta* was netted by D. Henne alighting on a small *Diplacus* bush at the edge of the marshy meadow.

A return trip to Plantation in May, 1967 proved to be far more productive. Prior to this Oakley Shields had determined the host plant of the closely related *Annaphila miona*, as stated previ-

ously, which was of great assistance in tracing the possible host plant of *casta*. The ecology of the few known localities where this species occurs was beginning to display a more comprehensive picture, as the Plantation locality was comparable to the McDonald Forest area and also ties in with Walshingham's description of a "clearing in the redwoods".

The author and his wife arrived at the Plantation locality on May 15, 1967 and stationed themselves at strategic observation points at either end of the marshy meadow. This habitat is surrounded by tall, second growth redwoods (*Sequoia sempervirens*). Other trees include Madrone (*Arbutus menziesii*), Tanbark Oak (*Lithocarpus densiflora*), and *Ceanothus*. The predominant low vegetation consists of *Carex*, *Stachys*, *Iris*, *Diplacus*, *Mimulus*, *Dentaria*, *Trillium* and an unidentified low-growing, flowering perennial. There is a considerable amount of partially decayed, fallen redwood trunks and branches and first-growth stumps from past lumbering operations. Part of the meadow contains shallow water where *Stachys*, *Mimulus* and *Carex* predominate.

The day was sunny with a slight westerly breeze. The meadows do not receive the full sun until mid-morning, and the first adult activity of *Annaphila casta* did not occur until around 11:30 A.M. when one female was seen flying slowly low over the meadow and alighting periodically on *Carex* stems or dry vegetation with wing action typical of the Genus. This specimen was netted and placed alive in a screened container with the "presumed food-plant", a slimy-leaved, marsh inhabiting *Mimulus*, later identified as *Mimulus mochatatus* Dougl. Between noon and 12:45 P.M., ten more females were taken — all in fresh condition. Their flight pattern was similar to the first specimen collected and they were always in close association with young *Mimulus* plants. No females were actually observed in the act of oviposition, but upon examination of many young plants, 20 ova were found on the underside of the leaves that without much doubt were those of *casta*. The confined female laid three ova at random, probably due to artificial and disturbing conditions when in confinement. These were compared with those taken later on the underside of the *Mimulus* leaves with the use of a hand lens and were found to be identical. Unfortunately a detailed structural study of the ova was not made at this time, but we intend to add this at a later time in a subsequent publication as well as the full descriptions and illustrations of the larva and pupa now completed by Dr.

John A. Comstock. No adults were observed visiting flowers for nectar.

Growing plants were transported to the home laboratory as well as a good supply of leafy stems which were placed in a plastic bag and later put in refrigeration. This supply remained in good condition throughout the life cycle of the larvae. Two last instar larvae were transferred to *Mimulus guttatus* (*A. lithosina* host plant as recorded by J. S. Buckett) as an experiment, and it was readily consumed, but it will be determined by further experimentation whether this substitute foodplant will be accepted by newly hatched larvae.

The question presented itself as to the method of pupation of *Annaphila casta* in its highly specialized environment. The possibility of the larvae entering the soil in a marshy area was highly improbable, as many of their host plants where eggs were found were in heavy mud or even where a shallow covering of water occurred. The entering of dried sedge (*Carex*) stems or other pulpy stems, which is an adaptation of *Annaphila depicta morula* Rindge & Smith as recorded by Wm. Evans and *A. depicta depicta* Grt. larval behavior as followed by Comstock and Henne, seemed problematical, as very little of this material was available in close proximity to the breeding grounds, or even later in the season with the possibility of the drying out of the marshy areas. The most plausible solution seemed to be that the larvae might enter the relatively soft, partially decayed, fallen trunks and branches or bark or redwood. Samples of all likely material of this type from this habitat were transported to the laboratory, and the larvae, as it was surmised, entered this medium in the rearing cages and formed pupal cells made partially with chewed wood particles cemented together similar to those formed by the *A. astrologa* B & McD group. The larvae of *lithosina* were also found to have similar habits, and with *miona* having a comparable type habitat to *casta*, this species is also presumed to have the same type of adaptation in the pupal stage.

Rindge and Smith (1965) show that the genitalia of *miona* and *casta* prove their close relationship. Further studies by Wm. Bauer and J. S. Buckett, who have contributed a great deal of important knowledge on this interesting Genus, have further substantiated the *lithosina*, *miona*, *casta* relationship.

The evolvement of this complex presents an interesting challenge for further research.

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STUDIES IN LIFE HISTORIES OF NORTH AMERICAN LEPIDOPTERA CALIFORNIA ANNAPHILA III

JOHN ADAMS COMSTOCK¹ and CHRISTOPHER HENNE
Del Mar, California and Pearlblossom, California

IN CONTINUING THE LIFE HISTORY studies of California *Annaphilas* we have been fortunate in obtaining information on three species, the early stages and host plants of which have heretofore been unknown. These are *Annaphila lithosina* Hy. Edw., *Annaphila casta* Hy. Edw., and *Annaphila miona* Sm.

ANNAPHILA LITHOSINA Hy. Edw.

This species has been discussed by Rindge and Smith (1952) as one ranging through "northern and central California for which the early stages and foodplant are unknown."

Bauer, Buckett and Gardner observed the ovulation of *lithosina* near the American River, 3.5 mi. east of Auburn, El Dorado Co., Calif., el. 1000' in May, 1967 as recorded by Buckett. He had the larval host plant identified as *Mimulus guttatus* Fisch, ex D. C. He obligingly relayed this information to the associate author, who subsequently located still another colony of this species 6 mi. east of Auburn, Placer Co., el. 2000'. Field work in these two localities produced ova for the following early stage descriptions.

The eggs were found on the under surfaces of the terminal leaves and a few on the flower buds and stems.

Ova were collected in various stages of incubation with the progressive color changes recorded. Three females were observed in the act of ovulation.

EGG. (Fig. 1A)

Ovoid. Width, 0.5 mm.; approximately 0.35 mm. high. Surface covered by approximately 60 ridges arising at base and running toward micropyle, with many pinched out superiorly. The surface is straw-colored when freshly laid, later turning red-brown, and finally translucent gray prior to hatching.

Our figure is tipped slightly forward to show the micropylar area.

The egg under study hatched June 3, 1967.

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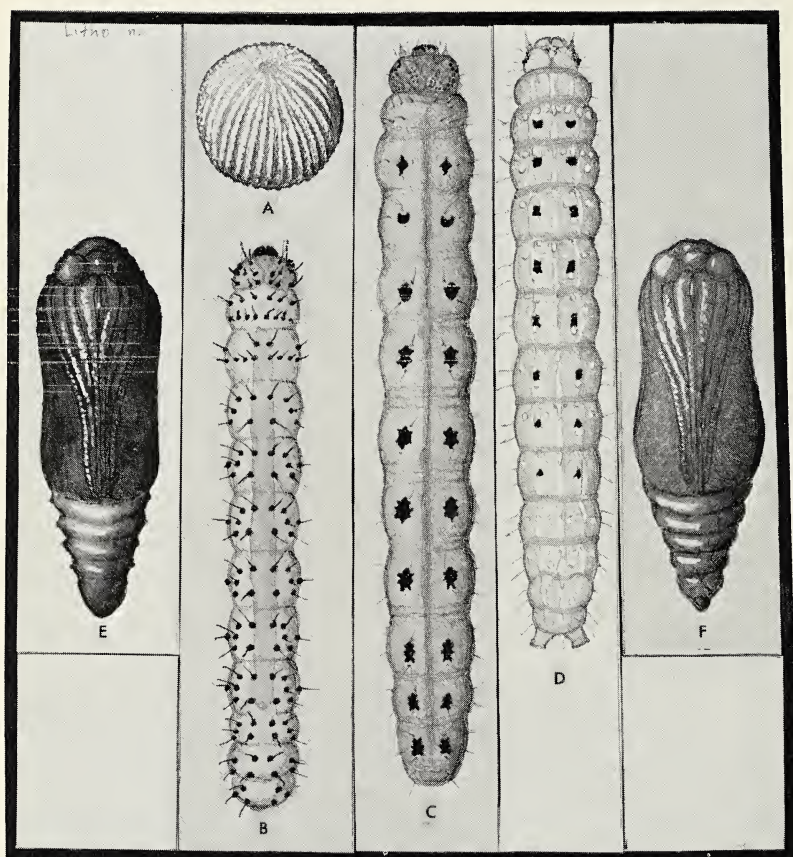


Fig. 1 Early stages of *Annaphila lithosina* and *A. casta*. *A. lithosina*: egg (A), 2nd larval instar (B), final larval instar (C), pupa (E). *A. casta*: final larval instar (D), pupa (F.)

FIRST INSTAR LARVA.

Length, 1.5 mm. Head, jet black. Width approximately 0.25 mm. Antennae translucent. Numerous small hyaline setae on the head which we have not attempted to map.

Body, width 0.2 mm.; cylindrical, translucent. First thoracic segment has a prominent dark cervical shield, with several raised black papillae on it. Second and third segments crossed transversely, each with a row of black papillae bearing long black setae. The remainder of the segments bear raised black papillae in essentially the same pattern and positions as with the second instar. Legs, darkest on tips, grading to body color proximally.

SECOND INSTAR LARVA. (Fig. 1B)

Length, 5.5 mm. Head width approximately 0.3 mm.; color, dull yellow-green, with numerous raised black papillae, each bearing a short straight seta; mandibles and ocelli, black.

Body, first segment pale yellow to white, crossed transversely by two rows of raised black papillae, most if not all of which bear short black setae. This, and most if not all of which bear short black setae. This, and most of the other segments wider than head. From the 2nd to 8th segments there is a longitudinal greenish area or band, suggestive of a full alimentary subsurface canal filled with bright green vegetation. The lower half of the body and the last three caudal segments are a translucent white. The typical body segment has two transverse rows of raised black papillae, each having moderately long black setae. Legs, soiled yellow on distal segments grading into translucent white proximally. Prolegs similarly colored.

FINAL INSTAR LARVA. (Fig. 1C)

Length, 24 mm. Head, width 1.6 mm. Tips of ocelli, yellow-green; tips of mandibles black. Numerous dark brown spots occur over the crown. Setae, translucent, some apparently arising from brown papillae or spots. Antennae, white.

Body, ground color green. A clearly definable longitudinal gray stripe runs from 2nd thoracic segment to cauda. A similar, though less well defined stripe runs suprastigmatically. Dorsolaterally a row of large black spots runs from 2nd thoracic to 11th segments, one to a segment on each side.

There may be some variation in the number of these spots, particularly if they occur on the penultimate instar.

Prior to pupation the larvae becomes a deep red-brown.

PUPA. (Fig. 1E)

Length, 10.5 mm.; greatest width through center 3.75 mm.

Length from cephalic tip to wing margins, 7 mm.; maxillae terminating 9.5 mm short of wing margins; antennae extending to approximately 1 mm. from distal edge of wing.

The head; appendages, eyes and wings, brownish-black, until the time of hatching when they become black. Their texture is finely rugose. Eyes relatively large. The dorsal portion of thorax and all abdominal segments are brown, and their surface texture smooth and glistening. Spiracles, black, their tips slightly protruding.

There are no spines, hooklets, or protruding structures on the cremaster.

ANNAPHILA CASTA Hy. Edw.

This rare noctuid ranges in certain restricted localities of northern California and southern Oregon in areas in association with marshy meadows and clearings, occurring within the coastal redwood and other coniferous forests.

Our examples were collected in the field, on the under side of leaves of young *Mimulus moschatus* Dougl. ex Lindl. at Plantation, Sonoma Co., Calif., el. 800', May 15, 1967.

Unfortunately neither a detailed structural study of the ova was made at that time nor a description and illustration of the first instar larva. However, a few brief notes were made on these two stages that might prove helpful for the continuation of life history studies on this species. They are as follows:

The ova collected in the field were found on the under side of the leaves of young *Mimulus moschatus* plants. They were deposited singly, usually only one to a leaf, but in two cases, three to a leaf were found. The number of ova per leaf is probably dependent upon the relationship of the number of ovipositing females to the number of plants available.

The ova are seemingly greatly protected by the rather heavy pilose structure on the under surface of the *Mimulus* leaves. Care has been taken by the female to secure them to the *Mimulus* leaves, in close proximity to the intersection of the leaf veins. The egg is pale yellow when freshly laid, later turning to a dark gray prior to hatching.

A casual examination of the young larvae showed them to be of light coloration, with dark heads and setae. They were feeding in the rearing cage on the under surface of the leaves in the central section and skeletonizing them between the veins. Seemingly there was a light webbing over the feeding area, as observed without the aid of a lens, and the larvae were quite

active when examined. It was considered important not to disturb them at this stage of development.

INTERMEDIATE INSTAR LARVA.

Measurements were not determined, as the larva under study was in pre-molt stage, and it was considered inadvisable to disturb the specimen.

Ground color, pale green with a lighter mottling and whitish punctations throughout surface body, similar to those more carefully described in the last instar. The only distinguishing markings are light, diagonally placed subdorsal punctations (2 pair per segment) and a fine light dorsal line. A suggestion of the curved dark dashes on the head is present.

Note: One out of eight larval specimens contained small black subdorsal spots (one pair per segment, but lacking on first three segments), seven in number, and including the pair of diagonally placed whitish punctations present on later instars.

FINAL INSTAR LARVA. (Fig. 1D)

Length, 12-20 mm., width, 3 mm.

Head width, 2 mm. Shining green with brownish cast. Ocelli, black; antennae pale yellow-green; front spotted brown; mandible dull green. An inward curved brownish-black dash runs on both sides of the head on dorsal surface, and continues laterally the width of the cervical shield.

Body, subcylindrical, tapering abruptly at caudal extremity where the body width is somewhat wider, and also gradually tapering to a rather flat head. The body is also considerably more robust and more uniform in width throughout than that of *lithosina*, which has an obvious taper from head to cauda.

Ground color, yellowish green with minute lighter mottling over body surface as seen under a lens. A narrow yellowish dorsal band appears running the length of the body. Minute yellowish-white punctations occur laterally, and another series appears below the infrastigmatal line, and still another series of twin whitish dots, or punctations, are placed diagonally below these. Dorsal markings are very distinctive. A series of large, black semiquadrate irregular spots occur in the subdorsal region, eight to ten pairs in number (two per segment). A whitish spot occurs on one of the diagonally placed pair of punctations and is surmounted by a short colorless seta. This is included in each of these large black spots, occurring posteriorly on these from segments 3-10, anteriorly on segments 1-2. The caudal segment

contains a smaller black spot, centered by a whitish somewhat raised punctuation.

As an experiment, two last instar *Annaphila casta* larvae were placed on a *Mimulus guttatus* plant, the native host of *Annaphila lithosina*, and it was found that they readily accepted this as a substitute for *Mimulus moschatus*.

One of the specimens under study was beginning to develop slight brownish coloration and had completed feeding. This undoubtedly was prepupal behavior, so it was placed in a rearing cage with a complete ecological environment typical (as far as possible) of the species natural environment, including soil, redwood bark and partially decomposed wood. This larva and seven additional specimens were found to enter the wood and excavate a cell for pupation, utilizing chewed wood particles cemented together as an outer covering, to form a cocoon.

PUPA (Fig. 1F)

Length, 11 mm. Greatest width through center 4.5 mm. Form similar to that of *lithosina* in many respects. Maxillae terminating at wing margins; antennae terminating 0.05 mm. short thereof; cremaster ending in a prominent round nodule, without spines or hooklets; spiracles concolorous with body, their surfaces not protruding.

The surface of head, thorax and wings slightly more rugose than that of *lithosina*. Abdominal segments glistening.

Color of the single pupa observed showed head, appendages, thorax, and wing cases nearly black with a brownish tinge. Abdominal segments red-brown.

ANNAPHILA MIONA J. B.. Smith

The field observations given us by Oakley Shields, who observed a female *miona* ovipositing on *Mimulus moschatus* Dougl., at Mather, Tuolumne Co., Calif., el. 4600', were a great help to us in obtaining material for our records on *Annaphila lithosina* and *Annaphila casta*.

Unfortunately we were not able to obtain ova or larvae of *miona* but intend to complete this study in a future publication.

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THE GENERIC, SPECIFIC AND LOWER CATEGORY NAMES OF THE NEARCTIC BUTTERFLIES

PART 6 — *The Genus Dryas*

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THIS GENUS PRESENTS few generic nomenclatorial problems once Hübner's earlier invalid and later valid use of the name *Dryas* is understood. This situation is discussed in the "Note" for *Dryas*.

Different spellings for the specific names have plagued this genus from early times.

Certain of the specific names of this genus were listed by early authors under the generic names *Papilio* Linnaeus and *Cethosia* Fabricius but these usages are presently considered to be only of historic interest.

LIST OF GENERIC NAMES USED OR AVAILABLE FOR DRYAS

DRYAS Hübner.

Type. julia (Fabricius).

COLAENIS Hübner.

Type. julia (Fabricius).

DRYAS HÜBNER. [1 Jan. 1807] - [19 Dec. 1807]¹. Samm. Exot. Schmett. 1: pls. 43-44. Hübner included "Dryas phalerata julia" and "Dryas phalerata vanillae" in the plates of this date.

Type. P[apilio]. N[ymphalis]. 2P[haleratus]. julia (emendatio) Fabricius. [17 Apr.] 1775. Syst. Ent.: pp. 509-510, no. 281.

Type Selection. Hemming. 1934. Entomologist. 67: 156. He said: "Type. - Papilio julia Fab., 1775." 3

Note. Hübner on page [1] in the "Tentamen" [1806] used the name *Dryas* for paphia Linnaeus which became its type species; as the "Tentamen" was declared an invalid work by the International Commission, the use of the name Dryas in that work was also invalidated. The name, however, was still available for use.

COLAENIS HUBNER, [1819]⁴. Verz. Bekann. Schmett. (2): 31-32, no. 5. He included among other: "259. Colaenis Julia Fab. . ."

Type. P[apilio]. N[ymphalis]. P[haleratus]. julia (emendatio) Fabricius. [17 Apr.] 1775². Syst. Ent.: pp. 509-510, no. 281.

Type Selection. Scudder. [8 Apr.] 1875⁵. Proc. Amer. Acad. Arts Sci. 10: 146, no. 280. He said: "Julia may be taken as the type."

LIST OF SPECIES AND LOWER CATEGORY NAMES USED OR AVAILABLE FOR DRYAS

1. DRYAS JULIA (FABRICIUS).

alcionea (Cramer).

carteri (Riley).

cillene (Cramer).

delila (Fabricius).

julia (Fabricius).

moderata (Stichel).

nudeola (Stichel).

1. DRYAS JULIA (FABRICIUS).

alcionea, Pap[ilio]. Helicon[ius]. Cramer. [1779]².

Uitland, Kapellen. 3(18): 38, nos. A, F-G; pl. 215, figs. A, F-G. The name is also listed in the index 3(24): 173. [1780]². ["in Suriname"] (see cillene, p. 38, nos. D-E for habitats of all species given on Plate 215). Male and female described. No series nor date data given. Herbst. 1790. Natursyst. Schmett. 4: pl. 67, spelled alcylene (in error) (see Strecker 1878, Butt. Moths N. Amer., Compl. Syn. Cat. Macrolepid.: p. 108, in no. 184).

carteri, C[olaenis]. julia N. Riley. Sept. 1926.

Entomologist. 59(760):240; pl. 2, fig. 1. "It is represented by 10 ♂♂, 5 ♀♀ in the B. M., the type ♂ and ♀ coming from Nassau". No date data given.

cillene, Pap[ilio]. Helicon[ius]. Cramer. [1780]².

Uitland, Kapellen. 3(24): 173. Described and figured earlier [1779]² without a generic name in Pt. 18 on page 38, as nos. D-E, and on Pl. 215, as figs. D-E. Habitat "in Suriname". No sex, series nor date data given. Fabricius, 1781. Spec. Ins. 2: 100, no. 439 gave as P. N. P. cellene (lapsus calami). Fabricius, 1796. Index Alph. . . Ent. Syst.: p. 121, no. 176 gave as Papilio F. cellene (lapsus calami).

delila, P[apilio]. N[ymphalis]. P[haleratus]. Fabricius. [17 Apr.] 1775². Syst. Ent.: p. 510, no. 384. "Habitat in America. No sex, series nor date data given.

Dos Passos. 1964. Mem Lepid. Soc. (1): 97, in no. 628c misspelled Fabricius' name as delia and wrongly attributed delila as a lapsus calami to Skinner, 1989.

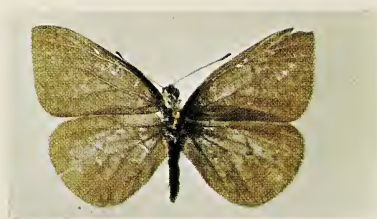
julia, P[apilio]. N[ymphalis]. P[haleratus]. (emendatio)
 Fabricus. [17 Apr.] 1775². Sys. Ext.:pp. 509-510,
 no. 281. "Habitat in America". No sex, series nor
 date data given. The name was originally spelled
iulia. Fabricius gave name as P. H. julia. 1793.
 Ent. Syst. 3(1): 180, no. 558.

moderata, Colaenis julia delila Stichel. 15 Apr. 1907.
 In P. Wystman. Genera Insectorum. (63): 12, in lc; p. 12,
 foot-note no. 3. "♂, typ. i. c. Stichel, N° 525, Honduras".
 No date data given. The name julia was given as iulia.

nudeola, Colaenis julia delila Stichel. 15 Apr. 1907.
 In P. Wystman. Genera Insectorum. (63): 12, in no. 1d;
 p. 12, foot-note no. 4. "♂, type. In Mus. Berol. N°
 1662. -Cuba". No date data given. The name julia was
 given as iulia.

FOOTNOTES

1. Hemming. 1937. Hübner. 1: 327-437. Gave data and dates for the Samm. Exot. Schmett.
2. Hemming. 1958. Official List Works Approv. Avail. Zool. Nomencl. (1): 9-10. Gave established dates for certain works of Cramer and Fabricius.
3. Hemming. 1937. Hübner. 1: 592-600. Gave data and dates for the "Tentamen".
4. Hemming. 1958. Official List Works Approv. Avail. Zool. Nomencl. (1): 4. Gave established dates for the Verz. Bekann. Schmett.
5. A copy of the work among the separates at the Allan Hancock Library (Univ. Sou. Calif.) (ex library, Boston Soc. Nat. Hist.) has the following printed label on the front wrapper: "Library of the Cambridge Entomological Club. Received April 8, 1875, by gift from the author."



A MELANIC FORM OF *PIERIS RAPAE*

THE SPECIMEN ILLUSTRATED ABOVE (upper side left and under side, right) was collected at Roseville, Macomb Co., Michigan, 29 May 1934. Arthur J. Yates.

Submitted by Julian P. Donahue, Dept. of Entomology, Michigan State University, E. Lansing, Mich.

Specimen from: Arthur J. Yates collection, M.S.U.

Reference: DONAHUE, JULIAN and M. C. NIELSEN. 1967 A melanic *Pieris rapae* from Michigan. *Mich. Entom.* 1:111-116.



MAN-MADE HABITAT FOR *COLIAS EURYTHEME*

THE ILLUSTRATION ABOVE shows a man-made habitat for *Colias eurytheme*. This is an alfalfa field in the southern part of the San Joaquin Valley of California. The field is being cut on the left. Adults are shown at flowers on the right. In this area, the frequency of white females, in contrast to orange-yellow females and males, was about 65% white indicating a gene frequency of about 40% for this dominant characteristic.

Submitted by W. Hovanitz

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A NEW SPECIES OF ARMYWORM
BELONGING TO THE GENUS *FARONTA* SMITH
FROM THE WESTERN UNITED STATES (NOCTUIDAE)
JOHN S. BUCKETT

Systematic Entomologist
California Department of Agriculture
Sacramento, California

FOR A NUMBER OF YEARS a dark brown species of *Faronta* Smith has been sent to the author for determination. This genus belongs in that section of the Noctuidae which contains economically important genera (e.g. *Pseudaletia* Franclemont, *Leucania* Ochseneheimer, etc.), and the species *Faronta terrapictalis* Buckett, new species, is a potential agricultural pest. Thus far, nothing is known of its life history, but judging by other species within the genus, the larvae are probably grass feeders. Of *F. diffusa* (Walker), Crumb (1956) states for larval hostplants "Feeds on various grasses and cereal crops showing a preference for the heads and a particular fondness for timothy."

F. terrapictalis occurs in the late spring, and has become more abundant in recent years. The largest series has been collected at Travis Air Force Base, Solano County, California, but apparently *terrapietalis* is widespread, records having been accumulated from Nevada and Oregon also.

***Faronta terrapictalis* Buckett, n. sp.**

Primaries with uneven ground color varying from tan to dark brown intermingled with grey areas; secondaries dark fuscus. Head with vertex and frons densely clothed with bicolored simple hairs, basally tan, terminally fuscus; palpi with tan and dark brown hairs ventrally, clothed in an admixture of tan and fuscus scales extrolaterally, dorsally clothed in light tan scales, terminal segment short; compound eyes round, densely hairy; antennae with scape and pedicle clothed in white broadened scales, flagellomere dorsally clothed in off-white and tan simple



Fig. 1 *Faronta terrapictalis* Buckett, Holotype male. Alturas, Modoc County, California, 15 June 1965. Note fuscous secondaries.

Fig. 2 *F. terrapictalis*, Allotype female. Travis Air Force Base, Solano County, California, 16 April 1964 (J. Gayden), CDA Slide No. 68G9-1.

scales, ventrally fasciculate with alternating short and elongate simple hairs per fasciculate bunch, terminally clothed in medium long hairs. Thorax with collar tri-colored, basally offwhite, medially with a dark brown transverse line, terminal portion chocolate brown; tegulae chocolate brown with tan longitudinal streaks, composed of simple elongated hairs; disc chocolate brown medially with tan longitudinal elongate hairs; ventral surface clothed in elongate tan hairs; legs with femora dorsally clothed in dark brown simple scales, ventrally with elongate tan simple hairs; tibiae with elongate brown scales and tan simple hairs; tarsae sparsely clothed with simple scales; ungues very slightly bifurcate; empodia greatly pronounced; primaries lacking ordinary transverse cross lines; costal area whitish, irrorated with black scales; radial and medial areas with tan scalation from region of transverse anterior area to subterminal line; a prominent white longitudinal line present on cubitus vein, extending from base to area of mediocubital sector, whence line becomes bifurcate on cubitus, and medius 3, reaching to subterminal line; area between cubitus and second anal vein slightly outlined in dark brown; subterminal line defined as differentiation in color between basal seven-eighths of wing and grey terminal area; terminal line represented as dark brown line at base of fringes; fringes composed of apparently three separate echelons of scales, these scales being tri-colored, basally tan, medially brown, apically white-tipped; veins in all foregoing described areas lightly outlined in dark brown when apparent; ventral surface dark brown; veins in terminal portion slightly outlined in black; costal area and basal intermarginal area irrorated with tan scales; fringes as in dorsal surface; secondaries smoky fuscus, veins only slightly outlined in black; fringes tri-color, basally dark brown, sub-basally tan, remainder white; ventral surface as in dorsal surface, but with veins more prominently outlined in black. Abdomen dorsally with dark brown simple hairs and scales, terminally with a few tan scales intermingled; ventrally clothed in tan and brown simple hairs, terminally hairs and scales becoming predominately tan in coloration. Greatest expanse of forewing 15mm. Genitalia as in figures 5 and 6.

Female: As in male but darker in coloration; antennae with flagellomeres ventrally ciliate; remainder as in male. Greatest expanse of forewing 16mm. Genitalia as in figure 9.

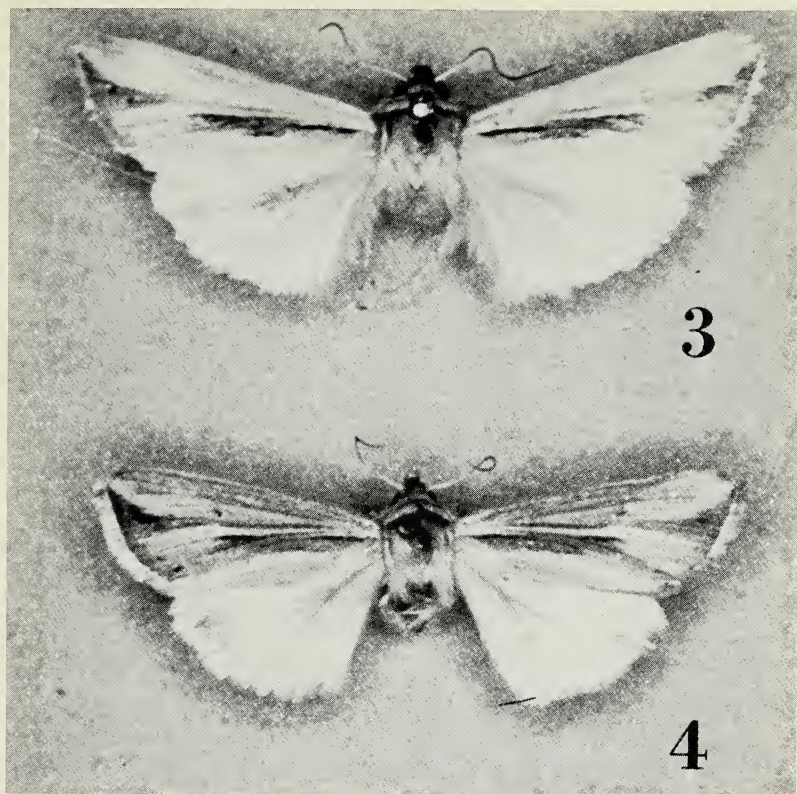


Fig. 3 *Faronta diffusa neptis* (Smith), male. 17 miles west of Roberts, Larimer County, Colorado, 30 July 1962 (J.S. Buckett and G.M. Trenam), Bauer-Buckett Slide No. 68C1-55. Note nearly white secondaries.

Fig. 4 *F. diffusa neptis*, female. Same locality and collectors as preceeding, Bauer-Buckett Slide No. 68C1-56. Note subterminal shade of secondaries.

SPECIMENS EXAMINED

Holotype male: CALIFORNIA: Alturas, Modoc County, 15 June 1965. Paratypes: 1 females, (designated allotype), Travis Air Force Base, Solano County, 16 April 1964, (J. Gayden); 2 males, same locality as holotype, 10 July 1960, 1 specimen bearing W.R.B.-J.S.B. slide No. 68C1-51; 1 male same locality as proceeding, 18 June 1963, silde No. 64E20-9; 2 males, Madeline, Lassen County, 14 June 1966, (R. P. Allen); 1 male Orinda, Contra Costa County, 28 April 1957, (S. F. Cook, Jr.); 1 male, Travis Air Force Base, Solano County, 13 May 1956; 2 males, same locality as preceeding, 25 March 1968 (F. R. Larson); 16 males, same locality as preceeding, 25 April 1968; 1 male, El

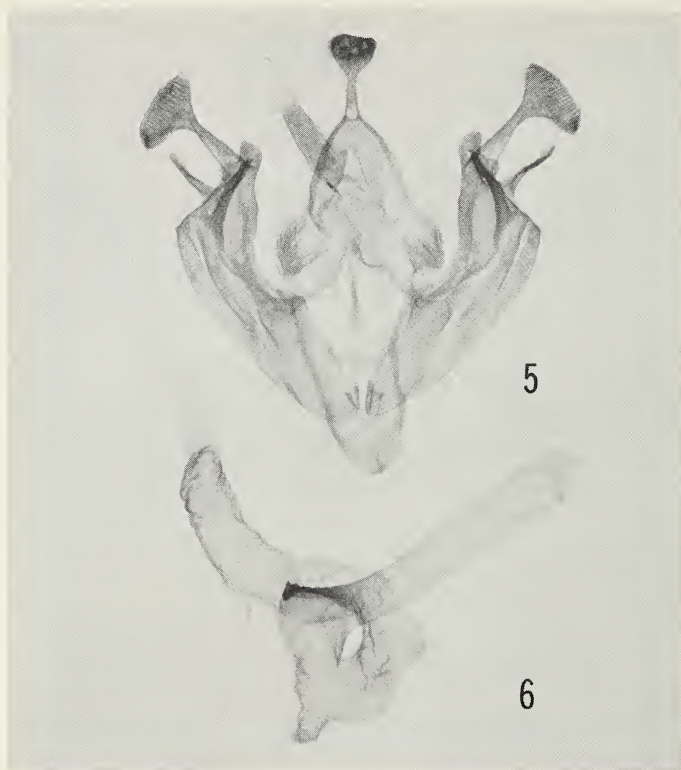


Fig. 5 *F. terrapictalis*, Paratype. Male genitalis minus aedeagus. Travis Air Force Base, Solano County, California, 25 April 1968 (J. Gayden), CDA Slide No. 68G3-21.

Fig. 6 *F. terrapictalis*, aedeagus. Same data as in Fig. 5.

Cerrito, Contra Costa County, 4 April 1961, (C. D. MacNeill), W.R.B.-J.S.B. slide No. 68B20-52; 1 male, Inverness, Marin County, 12 April 1940, (W. R. Bauer). NEVADA: 1 male, Winnemucca, Humboldt County, 29 May 1960, (T. R. Haig); 1 male same locality as preceeding, 5 June 1961, (R. C. Bechtel). OREGON: 3 males, Baker, Baker County, 5 June 1964, (K. Goeden.)

Holotype male deposited in the Type Collection, Department of Entomology, University of California, Davis; allotype female deposited in the insect collection, Bureau of Entomology, California Department of Agriculture, Sacramento, California. Paratypes deposited in the following institutions and collections: American Museum of Natural History, New York; Bauer-Buckett



Fig. 7 *F. diffusa neptis*, male genitalia minus aedeagus. Data same as for Fig. 3, except Bauer-Buckett Slide No. 68B20-51.

Fig. 8 *F. diffusa neptis*, aedeagus. Same data as in Fig. 7.

Collection, Davis; California Academy of Sciences, San Francisco; California Department of Agriculture, Sacramento; John G. Franclemont Collection, Cornell University, Ithaca, New York; Los Angeles County Museum of Natural History, Los Angeles; United States National Museum, Washington, D. C.; University of California, Berkeley and Davis.

I would like to extend my appreciation to those that made material available for this work, and particularly to Mr. George M. Buxton, Bureau of Entomology, California Department of Agriculture, Sacramento, for the photography and to my colleague Mr. William R. Bauer of the same Bureau for preparation of genitalia slides.

F. terrapictalis is most closely related to *F. diffusa*, as is evidenced by both the maculation, and similarity of the genitalia (see figs. 5, 6, 7, 8, 9, and 10). It can be superficially distinguish-

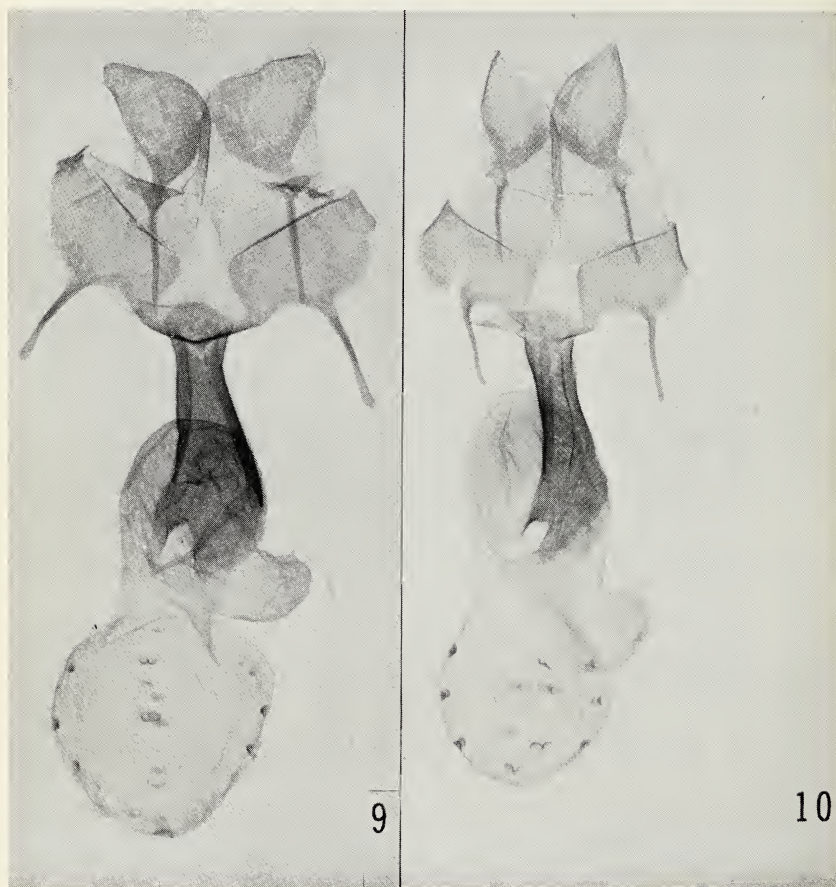


Fig. 9 *F. terrapictalis*, Allotype female genitalia. Data same as in Fig. 2.
Fig. 10 *F. diffusa neptis*, female genitalia. Same data as in Fig. 4.

ed from the latter by its dark brown coloration dorsally both on the primaries and the secondaries, whereas *diffusa* is "straw-colored."

LITERATURE CITED

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EARLY STAGES OF
LYCOMORPHA REGULUS GRINNELL,
WITH NOTES ON THE IMAGO.
(LEPIDOPTERA: AMATIDAE)

JOHN ADAMS COMSTOCK¹

and

CHRISTOPHER HENNE²

ABSTRACT

Lycomorpha regulus, a species of moth that feeds through its metamorphosis on a lichen, *Parmelia plittii* Gyrel, is discussed and its early stages illustrated and in part described.

INTRODUCTION

Lycomorpha regulus was described by Fordyce Grinnell in 1903, the type locality being Mt. Wilson, Sierra Madre Mountains, (San Gabriel Mts.) Los Angeles County, California.

Specimens have been collected from various localities throughout southern California, and its range extends into Arizona. Larvae have not yet been taken in the field.

Our examples were determined through the cooperation of Lloyd Martin, staff member in Entomology of the Los Angeles County Museum of Natural History. Determination of the food-plant was made by Dr. Mason E. Hale, Jr. Curator of Cryptogams of the U.S. National Museum, Smithsonian Institution. As usual, Dr. Reid Moran, Botanist of the San Diego Museum of Natural History, was helpful with other botanical determinations.

The series in the Los Angeles Museum collection, as well as in private collections, show considerable variation in maculation. However, for the present we are treating this as a single species in connection with our life history studies, because our reared specimens along with those collected in the field, appear to be reasonably constant. A detailed taxonomic study by a specialist in this group might further clarify the interrelationship of the *regulus*, *fulgens*, *grotei* complex.

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² Pearblossom, California.

An attempt was made by the associate author to rear this species from a confined female which had been collected in the Santa Monica Mountains, June 21, 1936 (elevation 1800 ft.) while the specimen was visiting moisture. Ova were laid in the rearing cage. The resultant young larvae were fed on the *Pamelia* lichen occurring on Valley Oak, *Quercus lobata* Neé in the Conejo region. The larvae fed on this species of lichen only when the plant was kept moist. During an interval in their 2nd instar when the lichen was allowed to dry, the larvae went into a state of aestivation which was assumed to be normal in their native state. Unfortunately laboratory conditions were not otherwise suitable and they all died during the winter months.

June 19, 1957, in La Sierra Canyon, Santa Monica Mountains (elevation 1000 ft.) a few specimens were observed on the wing during the heat of the day, but these avoided capture. Fortunately, Jerry Stidham, who was assisting with the field work, located a pool of water where several *Lycomorpha* specimens, as well as parts of others, were floating on the surface. Two of these were still alive. They were rescued, and in time fully dried their wings. The porous rocks in the immediate vicinity had a covering of *Pamelia* lichen. Specimens of this lichen growing upon small porous igneous rocks were taken back to the laboratory and placed in a rearing cage with a cloth wick running to a water container below. This technique kept the lichen continually damp. The confined females oviposited readily in the crevices of the rocks. The subsequent larvae fed through to maturity, emerging from August 30 to September 18 of the same year. No illustrations were made at that time.

Several more years elapsed before another opportunity occurred to complete the life history studies of this species. In September, 1967, through the cooperation of Luther Little of Juniper Hills, a female *Lycomorpha* was collected alive near his home (elevation 4800 ft.). The eggs laid the following day proved to be infertile, which probably signified that the specimen was out of its normal habitat because the preferred species of lichen does not occur in that immediate area.

A single specimen had been observed the previous year at the South Fork of Big Rock Creek (elevation 4500 ft.) visiting the flowers of *Lepidospartum squamatum* Gray. A field trip to that locality on September 27, 1967 proved most productive. The adult *Lycomorpha* were plentiful, visiting *Lepidospartum* flowers from mid-afternoon until sundown. Over fifty specimens

were collected on this date and on two subsequent trips, September 30 and October 18. All taken were females with the exception of one male collected when it was visiting the flowers of *Senecio douglasii monoensis* Jepson. This sex selection of two different attractant plants could be biochemically significant.

Several live females were confined in rearing cages with rocks containing *Pamelia* lichens occurring in the area. They oviposited in groups in the crevices, on the sides, and under the edges of the rocks that were placed in damp sand. In nature they probably lay eggs in similar situations in close proximity to lichen or upon bark.

The following descriptions, ecological photographs, and illustrations are the result of our investigations.

Adults emerged from January 25, 1968 to February 28, 1968 from ova of ten confined females. Sex ratio was approximately 2 to 1.

Larvae of different lots were highly variable — particularly as to the absence or presence of yellow spots along the middorsal line, and the intensity of spotting.

LIFE HISTORY

Ovum. (Fig. 1 A) Ovoid to round. Diameter 0.5 mm. Height 0.4 mm. on the average. The entire surface is lustrous white, and is completely covered with small round pits with raised walls and knobs. They showed some irregularity in shape probably due to the rough surfaces upon which they are laid. There is a slight cremasteric depression but no difference in the cellular covering.

First instar larva. (Fig. 1 B) Length, 2 mm. from tip of head to cauda, covered with many long curving setae, the length of each being 3 or more mm. in addition to numerous straight setae. Most of the long curving setae are black, and the short straight setae white.

Head, predominantly black, but the front, and area along the base, white. The ocelli are apparently black on a white base.

Body, hyaline-white, with a darker shading above the anal area. Spiracles prominent, giving the appearance of dark spots, relatively large at the anal end, and decreasing in size anteriorly. Legs and prolegs translucent.

No attempt to specifically map the setae has been used in our figure.

Second instar larva. (Described from a single individual, ex ova, So. Fork, Big Rock Creek, San Gabriel Mountains, Los Angeles County, Oct. 17, 1967, Elevation 4500 ft.)

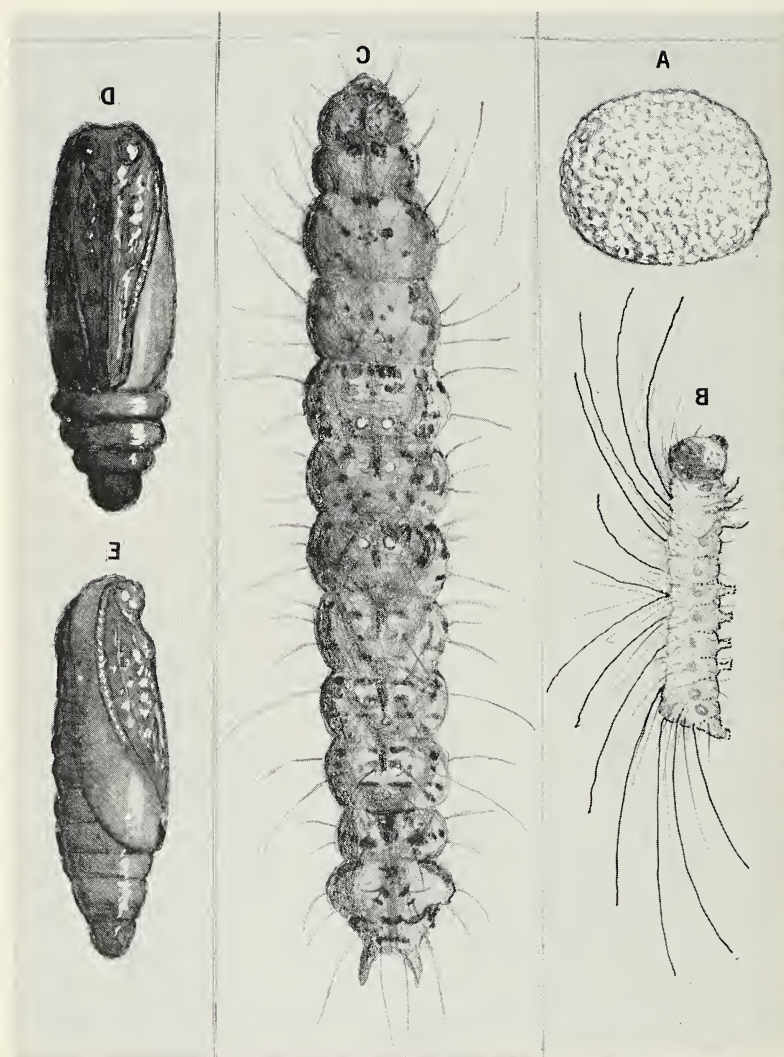


Fig. 1. Early stages of *Lycomorpha regulus*. Egg (A), 1st larval instar (B), mature larva (C), pupa (D and E).

Length of larva, 4 mm. Head width approximately 0.4 mm. mottled with black, bears a few short setae, ocelli predominantly black, some tinged with gray.

Body cylindrical, slightly wider than the head. Ground color of body dull green to greenish-yellow. The body surface is irregularly speckled along the middorsal area. It bears many setae, several in the middorsal area being long and black. Ventral area much darker than dorsal.

Third instar larva. (From same locality as the 2nd instar.)

Length of larva, 8 mm. Width of head, approximately 0.8 mm. Body ground color, soiled yellow, the surface covered by many black spots and irregular figures, no two segments being exactly alike. This spotting is too complex to describe, and description would be of little service in view of the wide variation in individuals.

Penultimate instar. A detailed description was not made. However, from a single individual it was noted that the maculation was similar to that of the mature larva, and an interesting and very distinctive marking appeared uniformly on the thoracic segments dorsally in the form of a light green cross.

Final instar. (Fig. 1 C) Length 14 to 18 mm. Width of average segment, 3 to 4 mm.

Head proportionately small, width 1.6 mm. Mandibles, tan, ocelli, black, labrum glossy tan, front pale green, lateral area also green. There are dark sooty markings over the upper third.

Body, robust, tapering to a small head and cauda. Surface expanded between segmental junctures, somewhat flattened ventrally.

Ground color, translucent bluish-green to olive green with entire dorsal and lateral surfaces covered by irregular dark brown to sooty-black markings, and raised punctations with centers of a lighter shade. Each is surmounted by a long fine seta. The longest of these issue from the thoracic region and curve anteriorly. From the caudal region they curve posteriorly. The shorter setae in the mid-section are both excurved and incurved. Small groups of light colored setae occur in the area of the intersegmental folds, curving ventrally. Two irregular yellowish-green patches occur middorsally, interspersed by transverse rows of black dots. One occurs in the region of the thorax, the other in the mid-section. Twin eye spots of a dark shade are seen on the segment between these patches. A modification of these yellowish-green patches occurs on the segments as the head and cauda are approached, and they are seen as twin yellowish-green dots or dashes, varying considerably in the three specimens of larva being studied. A lighter green patch, including a group of yellowish-green spots, appears dorsally on the

cauda. A suggestion of the middorsal line is in evidence only in this area and on the first two segments. The first three segments are of a more intense green than the olive-green seen on other dorsal parts of the body.

Entire ventral surface including prolegs are translucent dark bluish-green. Crochets, tan. True legs, glossy greenish-tan, bearing a few short pale colored setae. Spiracles dark.

Cocoon and pupa. A sheer whitish viscous light webbing closely covers the pupa. A larger, rather pale flat cocoon containing a few chewed particles of bark or other wood covers this and blends with its surroundings, which makes it difficult to detect. Seasoned pieces of Joshua Tree trunk containing old termite galleries (probably *Zootermopsis* sp.) were utilized in the rearing cages for pupation facilities. The many crevices in this material were ideally suitable for the construction of these highly adapted cocoons. In their natural habitat this species most likely seeks a similar environment in the form of crevices in bark, stumps or fallen logs.

Pupa. (Figs. 1, D and E). Length, 10.5 mm. Width through center, 3 mm. Fusiform, the base irregularly rounded, and cauda notably rounded with no protruding setae or spicules. Eyes relatively small and rounded. Antennae reaching to margin of wing cases. Color, brown — the head, appendages and cauda darker than the wing casts. Segmental junctures not clearly discernable in the anterior two-thirds owing to the irregular lobulation of the surface. Spiracles, inconspicuous, concolorous with body. The surface is covered on the abdominal side with minute shallow pits.

Addendum. The larvae are excellent examples of cryptic coloration, resembling the lichen and its surroundings. The adults can also be considered as a comparable example of so-called "warning colors" as they are very conspicuous while seeking nectar, generally on the yellow flowers of some species of *Composita*. Other members of this group of moths including certain of the *Arctiidae* are known to possess repellent properties that protect them against attack by predators.

Alvah Peterson, 1948, gives the habits and general characteristics of the *Amatidae*, to which *Lycomorpha* belongs, but does not specifically mention *L. regulus*.

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A PREVIOUSLY UNRECOGNIZED SUBSPECIES OF *PHILOTES SPECIOSA*

J. W. TILDEN

San Jose State College, San Jose, Calif.

GARTH & TILDEN (1963) included *Philotes speciosa* (H. Edw.) in the list of butterflies of the Yosemite on the basis of two specimens in the collections of the California Academy of Sciences, which had been presented by G. & R. Bohart. It was known at that time that these specimens represented an undescribed subspecies but description was postponed due to lack of material.

On April 24, 1966, Mr. John Lane took two specimens of this population at Briceburg, Mariposa Co., Calif., the locality where one of the previous specimens had been taken. On May 4-5 1968, Lane and Hughes collected the same area and took two more specimens including a female. These recent specimens indicate the existence of a population, though little known or collected. For this reason the following name is proposed.

Philotes speciosa bohartorum Tilden, new subspecies

General appearance: above, male larger darker and duller and with wider fuscous borders, than nominate *speciosa*. Female, entirely fuscous above with white fringes. Below, both sexes, whiter and with reduced spotting.

Holotype male: Forewing 9.8 mm. Scaling of wings thin, the dark markings of the under surface showing through the wing faintly. Ground color dull gray or fuscous, the blue overlay faint and never completely covering the gray. Fuscous borders wide, not sharply defined, grading gradually into the blue overlay of the discal area. Terminal line dark but not conspicuous against the dark ground color. Fringes white, narrow, darkened (checkered) at vein tips, more so on forewing than on hindwing.

Below white, a gray shade along anal margin of forewing. Maculation of forewing consisting of a postbasal spot on right wing (this spot missing on left wing); a moderate sized spot across end of cell; a small spot in cell R_2 ; a larger spot in cell $R_3 + 4$; similar spots in cells M_1 , M_2 , and Cu_1 , these five spots round or slightly oblong, nearly or quite filling the cells from vein to vein and forming a postmedian band of which the spot in cell $R_3 + 4$ is displaced inwardly. Maculation of hindwing consisting of an incomplete postbasal band formed of a small spot in cell $Sc + R_1$, a tiny dot at the base of the cell and a dark fleck on the anal margin; postmedian band of seven spots, the first in outer end of cell $Sc + R_1$, the second in cell R_5 (smaller and displaced outwardly), one small spot each in cells M_1 and M_2 (these displaced far outwardly), no spot in cell M_3 , a very small spot in cell Cu_1 (displaced far inwardly), a small spot in cell Cu_2 (directly below that in cell Cu_1), and a small dot in cell A_2 (displaced inwardly). This postmedian band is very irregular and could be interpreted as unrelated spots.

Antennae annulated white and black, apparently of thirty-two segments, of which twelve or thirteen form the club. Nudum of ten segments. Palpi white with black tips; legs whitish; under surface of abdomen whitish.

Allotype female: Forewing 10.5 mm. Upper surface entirely fuscous with no trace of blue. Fringes white, those of the forewing checkered, those of the hind wing uniformly white. Below white, a fuscous shade along the inner margin of the forewing. Maculation very similar in general pattern to that of the holotype. Fringes of forewing plainly checkered; fringes of hindwing with small dark points at vein ends. Antennae, palpi and legs essentially as in holotype.

Type material consists of six specimens. Holotype male, Briceburg, Mariposa Co., Calif., 24 April 1966, leg. J. Lane. Allotype female, same locality, 5 May 1968, leg. K. C. Hughes. One paratype male, same data as holotype. One paratype male, same locality, 4 May 1968, leg. J. Lane. One paratype male, same locality, 3 June 1938, leg. R. Bohart. The sixth specimen is labelled "Mariposa, Calif., 30 April 1932". The collector is not indicated but there is a label reading "Pres. by G. & R. Bohart". Since this specimen is not labelled as from Briceburg, it is not designated as a paratype.

Type locality: Briceburg, Mariposa Co., Calif. The specimens

were taken, as Mr. Lane has informed me (in litt.), just behind the Briceburg Station where an old bridge crosses the Merced River.

Variation in material at hand: The holotype and the two recent paratypes are nearly identical in coloration, but differ in size. One paratype is smaller (forewing 9.3 mm) and the other larger (forewing 11.0 mm) than the holotype. Both of the Bohart specimens are lighter in general facies. I ascribe this to fading with age. General appearance of the older specimens is very similar to that of the recent ones except that the wing surface of the older specimens is paler, causing the dark borders to stand out more clearly. There is very little significant variation among the specimens.

From nominate *Philotes speciosa*, *P. s. bohartorum* may be discriminated by its larger size, darker and duller dorsal surfaces, and more clearly white lower surfaces with reduced spotting. Dr. John S. Garth has a specimen of *Philotes speciosa* from Hume Lake in Kings-Sequoia National Park. I have not seen this specimen. It was captured too far from Briceburg to be included as part of the type material of *P. s. bohartorum*.

The type locality of *Philotes speciosa* (H. Edwards) is Havilah, Kern Co., California. The type is deposited in the American Museum of Natural History in New York. Except for the type, topotypical material has not been located. Dr. Alexander B. Klots of the American Museum kindly examined the type, and compared it with two males and three females labelled Mojave Desert, Kern Co., 2500 ft., May 14, 1914, and informed me that this material including the type, appeared to be reasonably homogeneous. It would seem that the type of *P. speciosa* is to be associated with the usual concept of this species as obtained from Mojave Desert material. It seems unlikely that the subspecies described in this paper could belong to the same population as the type.

A word may be said about the locality, Havilah. This now very small community was once the county seat of Kern County when horse stages skirted the foothills of the Sierra Nevada rather than crossing the valley which was at that time very difficult to traverse because of marshes and rivers. Havilah was then a center, and as is the case with many such pioneer stations, it is very likely that material taken at some distance from the actual town was labelled Havilah, since this was the only name

locality for some distance around. Only further study can determine if the type of *P. speciosa* came actually from near Havilah, or whether it in fact came from some distance away, but in any case, if the type resembles the material from Mojave, then the population from Briceburg is quite different.

Disposition of the type material: Holotype male and allotype female deposited in the Los Angeles County Museum as the gifts of Mr. J. Lane and Mr. K. C. Hughes. The Bohart specimens are returned to the California Academy of Sciences. One paratype in the collection of J. Lane and K. C. Hughes. The remaining paratype in the collection of the author.

This subspecies is named for Drs. G. & R. Bohart, the collectors of the first specimens, at the suggestion of Mr. John Lane. I am indebted to Mr. Lane and to Mr. Hughes for the loan of specimens, and to the California Academy of Sciences, through Curator Hugh B. Leech, for the loan of their material.

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Volume 6

Number 4

December, 1967

IN THIS ISSUE

- Life History Studies on the *Lithosina-Miona-Casta*
complex of the genus *Annaphila*
Christopher Henne 249
- Studies in the Life Histories of North American
Lepidoptera. California *Annaphila* III.
J. A. Comstock and C. Henne 257
- The Generic, Specific and Lower Category Names
of the Nearctic butterflies. Pt. 6, The Genus *Dryas*.
Paddy McHenry 263
- A Melanic form of *Pieris rapae* J. P. Donahue 266
- Man-made Habitat for *Colias Eurytheme* W. Hovanitz 267
- A New Species of Armyworm — Genus *Faronta*
J. S. Buckett 268
- Early Stages of *Lygomorpha regulus*.
J. A. Comstock and C. Henne 275
- A Previously Unrecognized Subspecies of *Philotes*
speciosa. J. W. Tilden 281



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